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Effet de la diversité des cultures sur les réseaux trophiques des arthropodes et la régulation du charançon du bananier par les prédateurs généralistes dans les systèmes pluri-spécifiques à base de plantain

Soutenue le 08 décembre 2014 devant le jury composé de

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AVANT-PROPOS

La diversité des plantes dans les agroécosystèmes soutiennent et procurent à la société humaine de nombreux services écosystémiques à savoir la pollinisation, le cycle des nutriments et le contrôle biologique des ravageurs des cultures. La perte de la biodiversité influence le fonctionnement des écosystèmes et peut avoir d'importantes conséquences sur la production durable des aliments et la séquestration du carbone. L'hétérogénéité des ressources et leur arrangement spatial peuvent modifier les caractéristiques des agroécosystèmes comme la biomasse, la pollinisation et le contrôle des ravageurs. La diversité des plantes cultivées modifie les réseaux trophiques des arthropodes et la régulation biologique des ravageurs des cultures.

En Afrique de l'Ouest et Centrale, la production du bananier plantain est souvent associée à des cultures annuelles (racines, tubercules, légumes, céréales) et des cultures pérennes (caféiers, cacaoyers, palmiers et autres…). Dans les agroécosystèmes à base de plantains, il peut y avoir jusqu'à plus de 20 espèces de plantes associées. La gestion des systèmes multi-espèces à base de plantain est souvent faite avec peu ou sans intrants agricoles. Dans les systèmes de production de bananes et de plantains, le charançon du bananier *Cosmopolites sordidus* Germar (Coleoptera, Curculionidae) est le plus important ravageur. La régulation biologique par les prédateurs généralistes semble la voie la plus prometteuse pour contrôler ce ravageur.

Ce travail de thèse a visé à comprendre comment la diversité des plantes cultivées dans les systèmes multi-espèces structure les réseaux trophiques des arthropodes. Nous avons étudié l'effet de la diversité des plantes associées au plantain sur la structure et le fonctionnement du réseau trophique et in fine la régulation de *C. sordidus* par les prédateurs généralistes.

Cette thèse est organisée en trois parties visant à :

(i) étudier de manière générale, l'effet de la diversité végétale locale (échelle parcellaire) sur le potentiel de régulation des ravageurs ;

(i) déterminer en conditions paysannes, comment la diversité végétale affecte la structure de la communauté des arthropodes ;

(ii) étudier l'effet des cultures fréquemment associées aux plantains sur la structure de la communauté des fourmis et le control de *C. sordidus*.

Ce travail a donné lieu à quatre publications (1 acceptée et 3 soumises) et une conférence :

PUBLICATIONS

Dassou G. Anicet, Sylvain Dépigny, Elsa Canard, Fabrice Vinatier, Philippe Tixier (2014). Contrasting effect of plant diversity across arthropods trophic groups and spatial extends: case of multi-specific plantain based agroecosystems (Basic and Applied Ecology, soumis).

Dassou G. Anicet, Dominique Carval, Sylvain Dépigny, Gabriel Fansi, Philippe Tixier (2014). Ant abundance and *Cosmopolites sordidus* damage in plantain fields as affected by intercropping. Biological Control, 81, 51-57.

Dassou G. Anicet, Dominique Carval, Sylvain Dépigny, Philippe Tixier (2014). Cultivated plant diversity and interspecific interactions drive the assemblage of the ant community in diversified plantain-based agroecosystems (Journal of Applied Ecology, soumis).

Dassou G. Anicet and Philippe Tixier (2014). Response of pest control by generalist predators at the field-scale to plant diversity: a meta-analysis (Agronomy for Sustainable Development, soumis).

CONFERENCE

Dassou G. Anicet, Sylvain Dépigny, Philippe Tixier (2014). Cropped plant diversity structures arthropod food webs in multi-specific plantain based agroecosystems. *Conférence annuelle conjointe British Ecological Society (BES) et la Société Française d'Ecologie (SFE) à Lille en France*.

Résumé

Dans les agroécosystèmes, la biodiversité fonctionnelle et la biodiversité associée fournissent de nombreux services à l'homme dont la pollinisation, la régulation biologique et le cycle des nutriments. L'association des cultures est une pratique agricole qui augmente la diversité des plantes dans les agroécosystèmes, fournit des ressources alimentaires alternatives et structure les communautés des arthropodes. Elle favorise les prédateurs généralistes pour la régulation biologique des ravageurs. Cette étude vise à comprendre comment la diversité des plantes, à l'échelle de la parcelle, structure les réseaux trophiques des arthropodes et peut participer à améliorer la régulation biologique des ravageurs. Tout d'abord, une méta-analyse a été réalisée afin de rechercher la relation générale liant la diversité végétale considérée à l'échelle locale et le contrôle des insectes ravageurs par les prédateurs généralistes. Ensuite, sur un réseau de 20 parcelles paysannes de la région de Njombé au Cameroun, nous avons étudié l'effet de la diversité des plantes cultivées sur la structure du réseau trophique des arthropodes. Les résultats ont montré que l'abondance des prédateurs était positivement corrélée avec la diversité des plantes alors que celle des herbivores était négativement corrélée avec la diversité des plantes. L'effet inverse de la diversité des plantes sur les abondances des prédateurs et des herbivores suggère que des effets top-down structurent la communauté des arthropodes dans les parcelles de plantain. Enfin, l'effet de trois cultures couramment associées au plantain (maïs *Zea mays*, macabo *Xanthosoma sagittifolium, et* pistache *Lagenaria siceraria)* sur i) la structure de la communauté des fourmis et ii) les dégâts de *Cosmopolites sordidus* ont été étudiés dans un essai réalisé en station expérimentale. Les trois cultures associées ont eu un effet significatif sur l'abondance de tous les taxa de fourmis collectés mais le sens et la magnitude de cet effet ont varié selon les taxa. Cela montre le levier que constituent les cultures associées pour structurer la communauté des prédateurs généralistes de l'agroécosystème. Les abondances de tous les taxa de fourmis étaient également corrélées avec les dégâts de *C. sordidus.* Les abondances de *Camponotus* spp., *Monomorium* spp., *Paratrechina longicornis* et *Tetramorium* sp. étaient négativement corrélées avec les dégâts de *C. sordidus* montrant leur potentiel de régulation de ce ravageur. Cette étude à l'échelle de la communauté de l'agroécosystème suggère qu'il est nécessaire de prendre en compte les effets de la diversité végétale à tous les niveaux trophiques pour espérer maximiser le service de régulation des ravageurs.

Mots clés : Diversité des plantes, cultures associées, réseaux trophiques, arthropodes, fourmis, structure de la communauté

Summary

Functional diversity and associated biodiversity in agroecosystems provide and promote important services to human society such as pollination, biological control, and nutrient cycling. Intercropping is a practical way to increase plant diversity in agroecosystems and participates to provide alternative foods and to structure arthropod communities, including generalist predators involved in pest control. To better understand how plant diversity structures the arthropod food web and how the control of pest may be optimized, we first made one meta-analysis to understand the mechanisms linking plant diversity to pest control by generalist predators at local scale. We second studied the effect of plant diversity on the arthropod community in contrasted plantain fields. We showed that predator abundance was positively correlated with plant diversity while herbivore abundance was negatively correlated with plant diversity. This strong and inverse effect of plant diversity on herbivore and predator abundance suggests that top-down forces structure the arthropod community in plantain fields and that it should be possible to structure the predator community to better control herbivores including pests. In a third step, we measured the effect of combinations of three associated crops maize *Zea mays*, cocoyam *Xanthosoma sagittifolium* and gourd *Lagenaria siceraria* as intercrops on ant community structure and then the effect relation between ant abundances with *Cosmopolites sordidus* damages. The three associated plants had a significant effect on abundance of all ant species but in different magnitudes and with either negative or positive effect showing that the selection of plant species that are intercropped is an efficient way to structure the ant community. The abundances of all species of ants were positively or negatively correlated with the damages of *C. sordidus* larvae. The abundances of *Camponotus* spp., *Monomorium* spp., *Paratrechina longicornis* and *Tetramorium* sp. were negatively correlated to *C. sordidus* damage. These ants appear to be the best candidates for *C. sordidus* control. These findings will help in the design of plantain agroecosystems that enhance pest control services.

Keywords: Plant diversity, intercropping, arthropod food webs, ants, interspecific interactions, habitat structure

Introduction Générale

1. Comprendre l'effet de la diversité végétale sur la régulation des insectes ravageurs par les prédateurs généralistes

1.1. Rôle fonctionnel de la biodiversité

La biodiversité se décline aux échelles des écosystèmes, des espèces, des populations et des gènes dans l'espace et dans le temps. L'anthropisation des écosystèmes est à l'origine d'une érosion de la biodiversité dans le monde (Thomas et al., 2004). Les activités humaines ont modifié la disponibilité des éléments des écosystèmes, la grandeur et la connectivité des habitats, la concentration du CO2 atmosphérique et la variabilité des variables climatiques. Ces changements contribuent à l'altération des mécanismes de stabilité, du maintien de la diversité et affecte indirectement le fonctionnement des écosystèmes (Hillebrand and Matthiessen, 2009). La baisse de la biodiversité pose des problèmes éthiques et esthétiques mais représente également un risque de dégradation des services écosystémiques. Selon les écologues, la diminution du nombre d'espèces devrait conduire à une altération du fonctionnement des écosystèmes (Loreau et al., 2001; McCann, 2000; Schmid et al., 2002), en particulier la productivité primaire (Loreau et al., 2001; Tilman, 1999), la rétention d'azote et la susceptibilité des invasions (Hector et al., 2001). Plusieurs mécanismes sont avancés pour expliquer la relation entre la diversité des espèces et le fonctionnement des écosystèmes :

i) l'effet d'échantillonnage (Tilman, 1999) où l'effet de sélection (Loreau, 2000) selon lequel les écosystèmes riches en espèces contiennent plus d'espèces très productives (Wardle, 2001),
ii) la complémentarité des niches (Leibold, 1995), qui explique que la diversité des espèces s'accompagne d'une diversité de leurs traits fonctionnels et donc de leur capacité à utiliser de façon complémentaire les différentes ressources disponibles pour assurer leur croissance,
iii) la différenciation des niches qui est définie comme un processus qui permet à deux espèces de partager certaines ressources sans qu'une espèce n'ait à rivaliser avec l'autre; ainsi, la coexistence est obtenue par la différenciation des niches écologiques réalisées. La séparation des niches ne peut se produire que s'il y a suffisamment d'espace géographique et écologique pour les organismes puissent s'y développer (Bertness and Callaway, 1994).

L'agroécologie mobilise aussi bien la diversité des plantes cultivées que la diversité des habitats et des espèces auxiliaires dans les cultures pour augmenter la durabilité des agroécosystèmes (Altieri, 1995; Baudry et al., 2000; Cardinale et al., 2003). La diversité des habitats augmente la diversité des espèces appartenant à tous les niveaux trophiques et participe notamment à réduire les risques d'invasion des ravageurs (Moonen and Barberi, 2008). La diversité des habitats via la diversification des plantes représente également un moyen de diversifier les productions et d'augmenter la multifonctionnalité des activités économiques (Naeem et al., 2012), ceci étant particulièrement important dans les agrosystèmes des petits paysans des pays du Sud (Snapp et al., 2010). En plus d'une possible production, la biodiversité fournit d'importants services à la société humaine à savoir la pollinisation, la régulation biologique, le cycle des nutriments, la production de nourriture et la séquestration du carbone (Altieri, 1999; Balvanera et al., 2006; Costanza and Folke, 1997).

La biodiversité peut se présenter sous plusieurs formes dans les agroécosystèmes. Dans les parcelles cultivées, la diversité végétale se décline en diversité cultivée, diversité associée (dans et autour des parcelles) et diversité spontanée (adventices). Le rôle des adventices sur la structuration des arthropodes prédateurs a longtemps été négligée, avec potentiellement des effets bénéfiques sur la communauté des prédateurs (Petit et al., 2010). Par exemple, des études ont montré que les prédateurs sont plus abondants dans les plantations de canne à sucre enherbées qu'en plantations désherbées (Ali and Reagan, 1985). L'ajout d'une plante de couverture dans les agroécosystèmes, qui représente un levier important sur la diversité végétale, participe à structurer les communautés des arthropodes (Duyck et al., 2011). La présence des arbres constitue aussi des habitats de l'entomofaune, leur caractère pérenne est un facteur de stabilité de la communauté des arthropodes (Halaj et al., 2000; Moran and Southwood, 1982). Les polycultures, largement pratiquées en zones tropicales, présentent par essence un niveau élevé de diversité végétale. Elles peuvent modifier l'abondance et la diversité des espèces à différents niveaux des réseaux trophiques (Ebeling et al., 2011). Elles enrichissent la productivité primaire nette (Hooper et al., 2005; Tilman and Downing, 1996) et fournissent plus de ressources alimentaires pour les arthropodes herbivores et augmentent aussi la biomasse des arthropodes consommateurs (Borer et al., 2012).

1.2. Description des mécanismes liant la diversité des plantes et la régulation des ravageurs par les prédateurs généralistes

Les systèmes agricoles se caractérisent par une biodiversité et une complexité plus faible que les systèmes naturels. Le service de régulation des insectes ravageurs résulte des interactions entre les

espèces de plante et d'arthropode de la communauté. Ces interactions (trophiques et non trophiques) sont largement dépendantes de la diversité, la dynamique temporelle et spatiale des producteurs primaires présentes dans le système. Des études récentes ont confirmé que la diversité végétale est un des principaux facteurs qui structure les réseaux trophiques (Scherber et al., 2010). La diversité des espèces végétales peut favoriser les ennemis naturels en leur apportant un abri, des hôtes et proies alternatives, ou encore une alimentation complémentaire (Landis et al., 2005). Il est généralement avancé que la diversité des plantes offre des micro-habitats et microclimats différents avec plus de possibilités d'abris aux ennemis naturels pour résister aux conditions défavorables (Landis et al., 2000). L'effet global de la diversité végétale sur la régulation des ravageurs est donc le 'bilan' entre des effets trophiques et d'habitat sur les ravageurs et les ennemis naturels, et la régulation proprement dite des ravageurs par les ennemis naturels. De manière théorique ce bilan n'est pas forcément positif. Selon les études de Haddad et al. (2001), la diversité des plantes est positivement corrélée avec l'abondance des herbivores. La relation positive entre la diversité des plantes et l'abondance des herbivores conduit une grande exploitation des plantes par herbivorie et une diminution de la productivité des plantes. Dans une méta-analyse en comparant les résultats de 31 articles publiés sur 10 ans, Tonhasca et Byrne (1994) ont montré une augmentation de l'herbivorie avec la diversité des plantes dans plus de 70% des cas. Plus récemment, Bommarco et Banks (2003) ont montré dans une méta-analyse basée sur une littérature couvrant une période de 18 ans que l'abondance des herbivores diminue et celle des prédateurs augmente dans des systèmes où la diversité de la végétation augmente. Dans la méta-analyse de Letourneau et al. (2011) sur 45 articles publiés sur 10 ans, il est également montré que la diversité des plantes réduit les populations des herbivores et augmente celles des prédateurs.

1.2.1. Effet de la diversité des plantes sur les habitats

- **Effet de refuges et de barrière dans les systèmes diversifiés**

Les systèmes diversifiés offrent des habitats, microclimats (Porté et al., 2004) et des abris aux ennemis naturels pour résister aux conditions défavorables. Les habitats fournissent aux arthropodes des conditions biotiques et abiotiques pour la reproduction et des refuges contre les perturbations des pratiques agricoles (Griffiths et al., 2008). Dans les habitats diversifiés, la diversité des plantes constitue une barrière pour les herbivores dans la recherche de leurs plantes hôtes. L'hypothèse de la concentration de la ressource proposée par Root (1973) suggère que la diversité des plantes diminue l'accessibilité à la plante hôte par les herbivores. Dans les systèmes diversifiés, les

ressources sont moins concentrées et donc plus difficile à détecter par les herbivores (Root, 1973). La concentration des ressources est favorable aux herbivores spécialistes parce qu'ils cherchent des habitats constitués essentiellement de leurs plantes hôtes pour y rester longtemps. L'hypothèse de concentration des ressources a été démontré par Baliddawa (1985) qui ont prouvé que les herbivores détectent moins leur ressource quand cette dernière est plus concentrée. Les herbivores ayant une dispersion active peuvent passer une barrière physique lorsque la plante hôte est physiquement cachée par d'autres plantes (Watt, 1992). Par exemple, des études on montré que le mil *Pennisetum glaucum*, a été utilisé pour constituer une barrière à la transmission de virus de mouche blanche *Bemisia tabaci* au niébé *Vigna unguculata* (Sharma et al., 1984) et au soja *Glycine max* (Rataul et al., 1989). Aussi, les herbivores peuvent être perturbés par la présence de plantes non hôtes ayant une forme ou une couleur différente qui limiterait l'apparence des arbres hôtes (Moore et al., 1988).

- **Effet de dilution dans les systèmes diversifiés**

La diversité des plantes augmente les ressources alimentaires dans les systèmes diversifiés. Les effets de dilution apparaissent lorsque l'abondance des herbivores n'augmente pas proportionnellement avec les taux de ressources alimentaires du système. Dans les systèmes diversifiés où les ressources sont denses les herbivores passent moins de temps sur les plantes que dans des systèmes avec moins de ressources alimentaires. En polycultures, la densité totale des plantes est plus élevée qu'en monocultures et les effets de dilution sont souvent à la base de faibles consommations des ressources par les herbivores sur les différentes plantes en association (Hambäck et al., 2014). Les systèmes dans lesquels il y a plus d'herbivores spécialistes on assiste aux effets de dilution qu'à la concentration des ressources (Otway et al., 2005). Des études ont montré que l'abondance des ravageurs de la culture de chou *Brassica* était considérément réduite quand les plantes étaient cultivées avec des pailles de trèfle (Finch and Collier, 2000).

- **Ségrégation de niche spatio-temporelle**

La ségrégation de la niche joue un rôle important dans le maintien de la biodiversité à différentes échelles spatio-temporelles en permettant à des espèces de coexister dans un même milieu sans entrer en compétition (Leibold, 1995). La diversité des plantes favorise a priori la ségrégation de niche en permettant à plusieurs espèces d'arthropodes de coexister. Chez les herbivores, on peut observer une ségrégation de niche dans les choix alimentaires; ce qui pourrait réduire la compétition

entre différentes espèces d'herbivores qui coexistent. Dans les systèmes diversifiés, chaque herbivore a la possibilité de faire le choix de sa ressource alimentaire en fonction de son régime. Les interactions compétitives entre les herbivores deviennent sévères quand plusieurs espèces d'herbivores ont le même régime alimentaire et des préférences pour les mêmes types de plantes (Belovsky, 1986). Dans les systèmes diversifiés, plusieurs espèces d'herbivores peuvent coexister dans le même habitat si elles ne partagent pas la même ressource alimentaire. La coexistence et des interactions compétitives peuvent être observées dans les communautés des prédateurs (Jacobs, 1977) et la coexistence peut être stable pendant plusieurs années entre les prédateurs. La ségrégation de niche peut s'observer chez les prédateurs au cas où ils n'exploitent pas les mêmes proies. La diversité des plantes augmente la diversité des herbivores (Haddad et al., 2001) et peut favoriser la coexistence entre plusieurs prédateurs.

- **Effet de la fragmentation des habitats**

La notion de fragmentation est tout phénomène artificiel de morcellement de l'espace, qui peut ou pourrait empêcher une ou plusieurs espèces vivantes de se déplacer comme elles le devraient et le pourraient en absence de facteur de fragmentation. A une grande échelle, la fragmentation des habitats est un processus important qui peut causer la perte de la biodiversité et l'extinction des espèces. La fragmentation des habitats n'influence pas uniquement l'abondance et la diversité des insectes mais modifie directement et indirectement les interactions biologiques entre les insectes et les autres organismes (Didham et al., 1996). La diminution de la diversité et de l'abondance des insectes par la fragmentation de l'habitat augmente au fur et mesure que l'échelle spatiale augmente. En effet, (Zabel and Tscharntke, 1998) ont montré que l'effet de la fragmentation de l'habitat sur les communautés des arthropodes suivait des mécanismes similaires aux échelles locale et du paysage, mais avec une moindre magnitude à l'échelle locale. La fragmentation des habitats affecte la dispersion des herbivores (Charrier et al., 1997). L'effet de la fragmentation est à relier avec les traits d'histoire de vie des arthropodes, notamment ceux associés à la dispersion. La fragmentation des habitats favoriserait la mortalité des insectes durant leur dispersion et réduit l'abondance des populations et la richesse de plusieurs espèces d'insectes.

1.2.2. Effet de la diversité des plantes sur la régulation 'bottom-up'

La régulation 'bottom-up' est une régulation ascendante où l'abondance d'un niveau trophique est limitée par le manque de ressource aux niveaux inférieurs. Dans les agroécosystèmes, on parle de 'bottom-up' principalement pour le contrôle par les ressources primaires (Hunter and Price, 1992; Power, 1992). Les effets 'bottom-up' sont très importants dans le contrôle des herbivores. Les plantes non hôtes peuvent constituer des obstacles physiques ou chimiques aux herbivores (Cook et al., 2007). Des cultures produites dans les espaces intra-parcellaires peuvent libérer des substances répulsives aux herbivores. C'est le cas de l'oignon cultivé dans les champs de la carotte pour réduire les attaques des mouches de carotte *Psila rosae* par une substance volatile répulsive libérée par l'oignon. Plusieurs plantes peuvent être utilisées comme des plantes pièges pour attirer des herbivores afin de réduire leurs dégâts sur les cultures principales. En Australie, le piment a été utilisé comme plante piège dans les parcelles du cotonnier pour réduire les dégâts de *Helicoverpa* spp. (Grundy et al., 2004). Toujours dans les parcelles du cotonnier aux USA, le sorgho a été utilisé comme plante piège pour réduire les dégâts des herbivores (Tillman and Mullinix Jr, 2004). Dans les systèmes diversifiés, il peut y avoir des effets allélopathiques qui affectent directement l'habileté des ravageurs à consommer les plantes hôtes (Ratnadass et al., 2012).

1.2.3. Effet de la diversité des plantes sur la régulation top-down

Selon la définition de Hairston et al (1960), l'effet top-down est la régulation descendante où chaque niveau trophique a le potentiel de réguler une proie appartenant au niveau trophique inférieur, indépendamment des ressources de la proie. Des modifications dans l'abondance des prédateurs peuvent avoir des conséquences sur la structure, le fonctionnement et la résilience des écosystèmes (Duffy, 2002). Dans les agroécosystèmes, la diversité des plantes structure les réseaux trophiques des arthropodes (Eisenhauer et al., 2013; Haddad et al., 2011). Elle affecte l'abondance et la diversité des espèces des réseaux trophiques (Ebeling et al., 2012; Loranger et al., 2014; Unsicker et al., 2006). Plusieurs études ont montré que la diversité des plantes a augmenté la régulation des ravageurs par les prédateurs généralistes (Quijas et al., 2010). Dans les systèmes diversifiés, l'abondance des prédateurs augmente dans les habitats créés par la diversité des plantes (Tylianakis et al., 2007). Dans les systèmes diversifiés, les ressources primaires peuvent jouer des rôles antagonistes vis-vis du de la régulation top-down. L'un des rôles est la fourniture des proies alternatives qui peuvent détourner les prédateurs généralistes. Les ressources primaires peuvent changer aussi le régime alimentaire des prédateurs généralistes en augmentant la prédation intra-guilde. La diversité des

plantes peut favoriser l'apparition des hôtes alternatifs et des proies pour les prédateurs généralistes (Bianchi et al., 2006). C'est le cas d'une compétition apparente que les écologistes appellent interaction négative <proie-proie> (Östman and Ives, 2003).

La diversité des plantes est donc un des facteurs principaux qui structurent les réseaux trophiques (Scherber et al., 2010) et pourrait constituer un levier pour améliorer la régulation des ravageurs par des prédateurs généralistes (Chaplin-Kramer et al., 2011; Letourneau et al., 2011; Quijas et al., 2010). Malgré son importance, la diversité et la structure des ressources primaires à l'échelle de la parcelle a relativement été peu étudiée. La diversité des plantes n'est pas forcément toujours une solution pratique généralisable dans toutes les conditions de productions, des effets négatifs sur la régulation des herbivores est parfois observés (Finke and Denno, 2004). Il est par conséquent important d'identifier dans quelles situations l'organisation de la diversité végétale permet de maximiser les régulations des ravageurs.

2. Le modèle d'étude et le réseau trophique des bananiers plantains

2.1. La production du plantain et ses contraintes

2.1.1. La production du plantain en Afrique et spécifiquement au Cameroun

Le plantain est une des plus importantes cultures vivrières en Afrique centrale et de l'ouest et en particulier au Cameroun. Il occupe une place primordiale dans l'alimentation de base de plusieurs pays d'Afrique et est la source d'hydrates de carbone qui est la plus importante dans les économies locales (Stover and Simmonds, 1987). La production du plantain contribue à la sécurité alimentaire et nutritionnelle dans la sous-région (Temple et al., 1996). Elle garantit de petits revenus aux producteurs du fait que sa production couvre toute l'année. Malgré son importance économique, la production du plantain est essentiellement extensive et le plus souvent plurispécifique en associations avec des cultures vivrières (maïs, arachides, niébé…), annuelles (racines, tubercules, légumes…) et pérennes (cacaoyers, caféiers, palmiers…) (**Photo 1**). Dans ces systèmes multi-espèces, la production du plantain se caractérise notamment par une faible utilisation d'intrants.

Photo 1: Exemple de systèmes de culture à base de plantain au Cameroun

2.1.2. Biologie du bananier plantain

Les plantains, comme tous les bananiers, sont des plantes géantes herbacées monocotylédone sans tige végétative aérienne de la famille des Musa et de l'ordre des Scitaminales (ou Zingibérales). Le bananier est originaire de l'Asie du Sud-est. Les bananes comestibles sont issues du croisement interspécifique entre deux bananiers sauvages, *Musa acuminata* de génome (AA) et *Musa balbisiana* de génome (BB). Les hybrides triploïdes comme le plantain (AAB) ont tendance à être plus vigoureux que les diploïdes ou les tétraploïdes (Gold et al., 2001). La tige souterraine (corme ou bulbe) est le lieu de formation des racines, des feuilles et de l'inflorescence. C'est à ce niveau que se différencient également les rejets, qui s'enracinent et se développe à leur tour. Le système radiculaire est fasciculé et l'émission de racines se fait durant toute la phase végétative. Le pseudo-tronc, ou faux-tronc, résulte de l'imbrication des gaines foliaires les unes dans les autres. Les fleurs sont toujours du même type, mais la conformation des inflorescences est très variable. L'inflorescence terminale apparaît à partir du méristème principal, apporté par une hampe florale, et fructifie pour produire un seul régime de bananes par plante. Lorsque la maturation des fruits est terminée, l'agriculteur coupe le régime, ainsi que la plante, ce qui va permettre à un ou plusieurs rejets issus du même rhizome de se développer (Lassoudière, 2007).

2.1.3. Les bioagresseurs et maladies du bananier

Plusieurs ravageurs et parasites infestent les bananiers dans leurs différentes zones de production. Parmi les maladies qui ont un impact économique majeur sur la production du bananier, il y a les maladies fongiques, notamment les cercosporioses (*Mycospharella fijiensis*, et *Mycospharella musicola*) et les fusarioses (*Fusarium oxysporum*), les maladies bactériennes, dues à *Ralstonia solanacearum* ou encore *Xanthomonas campestris*, et d'autres maladies virales (*Cucumovirus*, banana streak virus, banana bunchy top virus). Les ravageurs du bananier sont représentés par les nématodes, les thrips et les charançons, dont le plus redoutable est le charançon du bananier *Cosmopolites sordidus* (Lassoudière, 2007).

2.2. Le charançon du bananier

2.2.1. Biologie et écologie du charançon du bananier

- **Morphologie**

Le charançon du bananier, *C. sordidus* est originaire de l'Asie du Sud-est. Cette aire d'origine est similaire à celle du bananier (Stover and Simmonds, 1987). *Cosmopolites sordidus* s'alimente principalement sur les souches sauvages et cultivées du genre Musa (banane, plantain, abaca) (Gold et al., 2001). Il mesure de 9 à 16 mm de long. Sa cuticule est très dure et son rostre allongé.

- **Ecologie**

Les adultes vivent essentiellement dans les bananeraies, au niveau du sol et des détritus végétaux. Les adultes sont principalement retrouvés dans les résidus de culture et les environnements humides, comme les troncs coupés ou en décomposition, les bulbes coupés ou abîmés, ou cachés sous le sol (Pavis, 1988; Treverrow et al., 1992; Vilardebo, 1960; Vilardebo, 1973). Moznette (1920), Vilardebo (1960) et Treverrow et al. (1992) indiquent que les adultes sont en majorité associés aux troncs de bananiers, principalement dans les gaines des feuilles, autour des racines, sous les fibres à la base des plantes et occasionnellement dans les galeries larvaires

- **Biologie**

La femelle de *C. sordidus* pond approximativement 1 œuf par semaine et le sex-ratio est de 1 : 1. Elle dépose ses œufs, blancs et de forme ovale, un à un dans des trous qu'elle creuse à l'aide de son rostre (**Figure 1**). Elle pond généralement dans les gaines foliaires et à la partie supérieure du bulbe, en choisissant de préférence les plants qui ont atteint le stade de la floraison. La larve mesure 10 à 12 mm de long à la fin de sa croissance. Elle est apode, son corps est faiblement recourbé. Elle est de couleur blanc-crème avec une tête brun-rouge foncé et volumineuse, armée de fortes mandibules. Elle creuse des galeries à la périphérie du corme, leur diamètre augmentant progressivement. Les larves passent par 5 à 8 stades larvaires. La nymphe est blanche et mesure 12 mm de long. Les adultes émergents sont de couleur brun-rouge puis virent au noir lors du durcissement de l'exosquelette.

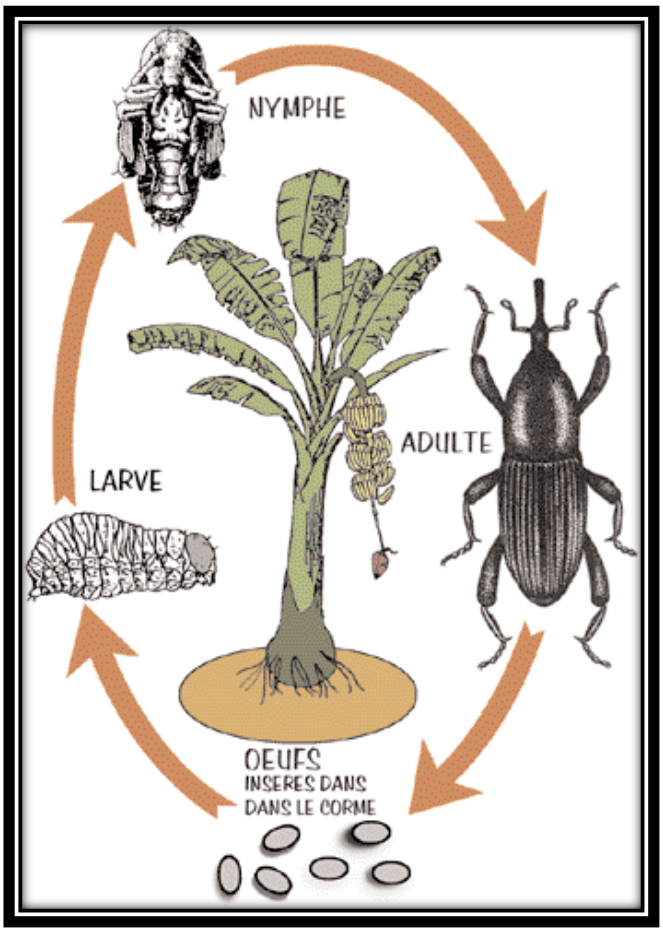

Figure 1. Cycle de développement du Charançon du Bananier (David Paulaud, Institut Agronomique, Nouvelle Calédonie).

2.2.2. Stratégies de lutte contre le charançon du bananier

- **Piégeage de masse**

Les pièges à phéromone contiennent de la sordidine qui attire le charançon du bananier mâle et femelle. Le piégeage de masse est une pratique efficace lorsqu'elle est employée à une échelle spatiale suffisante mais elle est assez peu adaptée aux petits producteurs de plantain à cause de la structure des parcelles et du coût de cette méthode.

- **Rotation culturale et prophylaxie**

L'utilisation de la rotation culturale avec des plantes non hôtes est aussi une pratique efficace (spécialement en association avec du piégeage de masse) mais n'est pas adaptée aux parcelles de petits producteurs de plantain. Malgré son caractère sédentaire et sa grande résistance au jeûne (Lemaire, 1996), le charançon se déplace massivement quelques mois après la mise en jachère (Rhino et al., 2010). L'utilisation de plants sains (vitroplants) permet de limiter la réinfestation des zones assainies par jachères.

- **Variétés de plantain résistantes**

Le plantain est particulièrement susceptible au charançon du bananier par rapport aux autres variétés de bananiers (Gold et al., 2001; Ortiz et al., 1995). L'utilisation de variétés de plantains plus tolérantes à *C. sordidus* serait particulièrement intéressante. Les différences de tolérance entre variétés sont assez mal connues et ce critère est quasi-absent des programmes d'amélioration variétale.

- **Régulation du charançon du bananier par les prédateurs généralistes**

Une grande diversité de prédateurs généralistes est présente dans les bananeraies, on y retrouve notamment fourmis, carabes, araignées, scolopendres, forficules, grenouilles et lézards. La classe la plus représentée, en termes de diversité et d'abondance, est celle des hexapodes, et surtout les fourmis (Hymenoptera, Formicidae). Aux Antilles françaises, dans les agroécosystèmes bananiers, il a été montré que l'addition d'une plante de couverture (doublement de la diversité végétale du système) modifie la structure des communautés des arthropodes notamment en déplaçant la niche trophique vers la nouvelle ressource (Duyck et al., 2011). Mollot et al. (2012) ont montré que l'ajout

d'une plante de couverture dans l'agroécosystème des bananiers augmente l'abondance de *Solenopsis geminata*, fourmis prédatrices de *C. sordidus* et augmente ensuite la prédation des œufs du ravageur. Certaines espèces de fourmis sont connues pour être responsables d'une forte régulation des populations de *C. sordidus* dans sa région d'origine (Abera-Kalibata et al., 2006) et dans certaines régions de production (Abera-Kalibata et al., 2008; Abera-Kalibata et al., 2007; Gold et al., 2001) avec des taux de prédation allant jusqu'à 70%, notamment au Cuba (Perfecto and Castineiras, 1998). Les fourmis sont des insectes sociaux capables de maintenir un niveau élevé de prédation étant donné que les excès de nourriture sont stockés dans le nid, et que les ouvrières continuent de prospecter pour de la nourriture même après satiété (Abera-Kalibata et al., 2008; Abera-Kalibata et al., 2007). Abera-Kalibata et al. (2006) ont observé la prédation des larves de *C. sordidus* par les fourmis *Myopopone Castanea* (Ponerinae). D'autres études ont montré que les prédateurs généralistes comme les fourmis, forficules, araignées sont des potentiels régulateurs biologiques de *C. sordidus* (Abera-Kalibata et al., 2006; Mollot et al., 2014). Dans les systèmes de culture, les communautés des fourmis sont complexes et ont des effets puissants sur les arthropodes de niveau trophique inférieur et sont souvent utilisées dans les programmes de lutte intégrée contre les ravageurs (Integreted Pest Management IPM) (Perfecto, 1991). Le potentiel de régulation biologique des fourmis dépend de la structure de leurs communautés et aussi du comportement de fourrage. En Martinique, Mollot et al. (2014) ont trouvé que les fourmis charpentières *Camponotus sexguttatus* consomment *C. sordidus* alors que Les fourmis *Odontomachus bauri* ont été aussi observées attaquées les larves de *C. sordidus* dans les résidus de bananiers (Carval, D., Communication personnelle). Au Cameroun, dans les bananeraies, les fourmis *Odontomachus* spp. ont été observées consommer les larves de *C. sordidus* (Okolle, J., Communication personnelle). Ces taxa d'*Odontomachus* spp. ont été attrapés sur les larves et les œufs de *C. sordidus* artificiellement placés sur les bulbes des bananiers comme appât (Abera-Kalibata et al., 2007). L'espèce *Odontomachus bauri* utilise ses longues mandibules pour attraper, immobiliser avec des substances toxiques et écraser ses proies (Patek et al., 2006). *Odontomadus bauri* est capable de changer de proies selon les espèces de proies abondantes. A Cuba, Roche et Abreu (1983) ont trouvé que les fourmis ont réduit les populations de *C. sordidus* dans des bananeraies qui étaient fortement infestées. En Uganda, Abera-Kalibata et al. (2008) ont trouvé que les fourmis *Pheidole* sp. et *Odontomachus troglodytes* Santschi ont réduit la densité des œufs de *C. sordidus*. Casteneiras et Ponce (1991) ont montré que les fourmis *Tetramorium guinensee* (Nylander) ont réduit les populations de *C. sordidus* et *Pheidole megacephala* (Fabricius) ont empêché l'oviposition des femelles de *C. sordidus* sur les bananiers. Au Kenya, les forficules du genre *Euborellia* ont été reconnus comme des prédateurs potentiels de *C. sordidus* (Koppenhöfer, 1993) alors que d'autres espèces de *Forficulina* ont été trouvées comme des prédateurs de *C. sordidus* dans les bananeraies

de l'Indonésie (Abera-Kalibata et al., 2006). Ces multiples études montrent l'importance des prédateurs généralistes, et notamment des fourmis, dans le contrôle biologique de *C. sordidus*. Il y a cependant très peu de travaux qui étudient comment la structure de la communauté (de fourmis ou le réseau trophique dans son entier) est susceptible d'être 'orientée' pour maximiser ces régulations.

3. Questionnements scientifiques et objectifs de la thèse

Cette thèse vise à comprendre comment la biodiversité cultivée et ou associée modifie la structure du réseau trophique des arthropodes et l'intensité de régulation du charançon du bananier dans les systèmes multi-spécifiques à base de plantains. Trois questions scientifiques structurent la thèse :

Question 1 : *De manière générale, quel est l'effet de la diversité végétale locale (échelle parcellaire) sur le potentiel de régulation des ravageurs ?*

La biodiversité joue un rôle majeur dans la régulation des fonctions des agroécosystèmes en particulier la régulation des ravageurs des plantes. L'effet de la diversité des plantes sur la régulation des ravageurs a largement été étudié ces dernières années. Un nombre croissant d'études montrent un effet important de l'organisation paysagère sur les populations de ravageurs et sur leur régulation. Par contre assez peu d'études traitent de l'échelle locale de la parcelle alors que c'est à l'échelle locale qu'interagissent les proies et les prédateurs. C'est aussi à cette échelle que les agriculteurs peuvent facilement modifier l'organisation spatiale. Pour combler ce manque, nous avons réalisé une méta-analyse sur l'effet de la diversité des plantes à l'échelle locale sur la régulation des ravageurs par les prédateurs généralistes. Notre méta-analyse vient compléter celle de Letourneau et al. (2011), en intégrant l'analyse d'articles majoritairement récents et pas seulement limités aux agroécosystèmes et en analysant les effets de la spécialisation des espèces, de l'échelle spatiale, et de la nature des habitats concernés.

Question 2 : *En conditions paysannes, comment la diversité végétale affecte la structure de la communauté des arthropodes?*

L'effet de l'organisation spatiale des plantes sur la structure du réseau trophique des arthropodes de la litière a été mesuré dans un réseau de parcelles afin de couvrir un gradient de complexité. L'objectif était dans chaque parcelle paysanne de caractériser la structure végétale (composition spécifique et structure spatiale) et celle des arthropodes. D'une part, nous avons utilisé les analyses isotopiques des arthropodes pour faire des groupes trophiques homogènes et étudier l'effet de la diversité végétale sur l'abondance de ces groupes trophiques d'arthropodes. D'autre part, nous avons étudié l'effet de la diversité végétale sur l'abondance des fourmis et la relation interspécifique entre les communautés des fourmis des systèmes de culture à base de plantain.

Question 3 : *Quel est l'effet des cultures fréquemment associées aux plantains sur la structure de la communauté des fourmis et le control de* C. sordidus *?*

Afin de mieux comprendre l'effet particulier des principales cultures associées aux plantains, nous avons mis en place une expérimentation en station expérimentale associant de manière simplifiée des bananiers plantains avec trois des espèces de plantes les plus couramment cultivées dans ces systèmes. En plus de simplifier les aspects spatiaux, cet essai visait à comprendre plus finement les mécanismes qui lient la communauté des plantes associées à celle des fourmis et aux dégâts de *C. sordidus*. Nous avons ensuite cherché à comprendre la relation qui lie la communauté des fourmis aux dégâts du charançon du bananier.

Chapitre 1. Méta-analyse : De manière générale, quel est l'effet de la diversité végétale locale (échelle parcellaire) sur le potentiel de régulation des ravageurs ?

Cette partie de la thèse vise à étudier de façon générale comment la diversité des plantes répond à l'abondance et à la diversité des arthropodes prédateurs et herbivores à l'échelle locale dans différents écosystèmes terrestres. Elle vise également à comprendre comment la diversité et l'abondance des arthropodes répondent à la diversité des plantes en fonction de la spécialisation des arthropodes et de l'échelle spatiale.

Cette partie repose sur une revue de méta-analyse qui est soumise à Agronomy for sustainable development et est intitulé **Response of pest control by generalist predators to field-scale plant diversity: a meta-analysis.** Pour faire la méta-analyse, nous nous sommes appuyés sur des articles qui traitent de l'effet de la diversité des plantes sur l'abondance et la diversité des arthropodes à l'échelle locale. Ces articles ont été recherchés dans la base bibliographique Web of Science selon une procédure standardisée (avec des mots clés bien précis). La recherche des articles a généré 559 abstracts à partir desquels 32 études ont été sélectionnés pour la méta-analyse.

Dans chaque étude, la grandeur de l'effet <effect size> de la diversité des plantes sur l'abondance et la diversité des arthropodes a été déterminée. Le premier objectif était de voir comment les herbivores et les prédateurs répondent à la diversité des plantes. Le deuxième objectif était de comprendre comment la spécialisation des herbivores et des prédateurs répond à la diversité des plantes. Le troisième objectif était de voir l'influence de l'échelle spatiale sur l'abondance et la diversité des arthropodes à la réponse à la diversité des plantes.

Response of pest control by generalist predators at the field-scale to plant diversity: a meta-analysis

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Abstract

Disentangling the effect of plant diversity on the control of herbivores is a major issue to improve the sustainability of agriculture. Recently, there were many studies that investigated the relationship between plant diversity and arthropod communities at landscape scale but there were fewer at local scale. We conducted a meta-analysis of 32 local scale studies which treated the relationship between plant diversity and arthropod communities. We found that predators have a strong positive response but the herbivores have a weak negative response to plant diversity. Plant diversity strongly increased the abundance of generalist predators. While the effects of the scale remain quite fuzzy, there was a trend for an increasing effect of the scale of observation on the response of specialist herbivores, while it was decreasing with the scale for generalist herbivores. There was no effect of the scale of observation on the response of generalist predators to plant diversification. Our results suggest that the response of herbivore to plant diversification is a balance between habitat and trophic effect that varies according to arthropod specialization and types of habitats.

Keywords: Plant diversity, local scale, effect size, biological control, specialization, predation, herbivores, pest regulation service

1. Introduction

Pest regulation services in agriculture depend on a complex suite of direct and indirect interactions involving multiples herbivores and predators (Cardinale et al. 2011; Stowe et al. 2000; Vandermeer et al. 2010). This function could be changed according to arthropod and plant communities (Duffy 2002). Agroecologists have suspected that increasing plant diversity within agricultural fields improve the structure of arthropod food webs by reducing herbivore abundance and crop damages (Andow 1991; Letourneau et al. 2011; Pimentel 1961). On the other hand, in more diversified agroecosystems, the predators may feed on more abundant alternative preys, thus decreasing the control on pests (Holt 1977). Disentangling the effect of plant diversification on pest control and the scale at which plant diversity affect this process remain key challenges for sustainable agriculture (Bianchi et al. 2006).

In the last decade, there were an increasing number of studies of the effect of plant diversity at the landscape scale (Fahrig et al. 2011; Tscharntke and Brandl 2004). In their meta-analysis Chaplin-Kramer et al (2011) demonstrated that the effect of landscape complexity on crop pest and natural enemy, showing that the effect depends of the type of organisms (including their status of generalist or specialist). We can hypothesise that the most appropriated scale of effect of plant diversity may strongly be related to life history traits (most especially dispersal traits) of both crop pest and enemy, and that in the case of medium to low dispersal organisms the local scale may have a prevailing influence. The level of intervention remains harder at the landscape scale compared to the field scale at which farmers directly manage communities. The major effect of local plant diversity on all communities was demonstrated in plant diversity experiments (Scherber et al. 2010). In their meta-analysis, Letourneau et al. (2011) showed (based on articles published between 1998 and 2008) that the diversification significantly tends to increase herbivore suppression and natural enemy abundance and to decrease crop damage at relatively small scale. In their analysis, they did not separate specialist vs. generalist enemy and did not address the issue of the scale of organisation of plant diversity. Furthermore, most recent studies were not incorporated in their analysis.

The role of plant diversity on generalist predators remains a key question in biological control (Altieri 1999; Moran and Hurd 1997; Ratnadass etal. 2012; Scheu 2001). Plant diversity may strongly influences omnivores, the level of intra-guild predation may potentially increase in more diverse ecosystem (Rosenheim et al. 1995; Rosenheim et al. 1993). Theories based on modelling tend to show that increasing omnivory lead to the reduction of the biological control of crop pests (Diehl and Feißel 2000; Polis 1991). Recent studies tend to moderate this finding; for instance, plant diversity experiments showed that abundance of all trophic groups increase with the plant diversity except

pests and invasive species (Scherber et al. 2010) or that the community is more dominated by predators as plant richness increases (Haddad et al. 2009).

The scale at which plant diversity is organized strongly influence its effect on communities (Stoner and Joern 2004; Thies et al. 2003) and more specifically pest control (Bianchi et al. 2006). Results from Chaplin-Kramer et al. (2011) suggest that the effect of plant diversification at local scale may be stronger on the abundance of some predators than larger scales. The importance of local scale was recently confirmed in the case of natural enemy (Sarthou et al. 2014). This seems particularly true for natural enemies that were shown to be best predicted at smaller scales than pests (Perović et al. 2010; Thies et al. 2005). In this article, we present a meta-analysis of the effect of plant diversity at field scale on the control of pests by generalist predators. We used the meta-analysis of 32 articles mainly published between 2001 and 2014 to ask how specialization affects herbivore and predator responses to plant diversity and how the scales of these responses may differ. Specially, we investigate following questions: i) How did plant diversity affect herbivores and predators abundance and diversity? ii) Do generalist predators, specialist and generalist herbivores respond differently to plant diversity? iii) Do generalist predators, specialist and generalist herbivores respond to plant diversity at different local scales?

2. Materials and Methods

2.1. Selection study

We selected the studies through a search on Web of Science last updated in June 2014, using the search string: ["plant diversity" OR "plant richness" OR "inter*crop*" OR "intercrop*"] AND ["predat*" OR "biological control" OR "pest control" OR "natural enn*" OR "pest"] AND ["agr*" OR "crop"]. Many studies have investigated the effects of plant diversity on herbivore control by generalist predators at local scale. Our goal was to synthesize the results from studies concerned plant diversity at local scale. Over 559 abstracts were reviewed for relevance and 32 studies were ultimately selected using the following criteria: i) the study treated the plant diversity or intercropping, ii) the agoecosystem scale of study was local, iii) statistics reported as the relationship between plant diversity and arthropod response.

2.2. Predictor variables

We defined several categorical and one continuous variable (scale).

1) Predators vs herbivores: It is the trophic level which specified whether the arthropod was a predator or an herbivore.

2) Response: it is the arthropod response which included abundance or diversity for the predators or herbivores and plant damage for the herbivores.

3) Habitat: it is the type of agroecosystem which included natural habitat, non-crop habitat and crop habitat.

2.3. Analysis

The statistic values Df, P, t, or r2 from each response reported in a study were converted in a standard statistic, the correlation coefficient r. Then, we compute Fisher's Z, using the equation of Rosenthal and DiMatteo (2002): **$Z = 1 / 2 \log[(1+r) / (1-r)]$**. Z estimates the magnitude of the relationship between a predictor variable and its response. In this search, we generated 175 effect sizes (Z) from 32 studies. We analyzed the relationship between the effect size and the variable responses using the Generalized Linear Models (GLM). Statistical analyses were performed with R 2.15.0 (R Development Core Team 2014) and we used an alpha level of 0.05.

3. Results

3.1. Predator and herbivore response to plant diversity

The total predators had a positive significant response to plant diversity (P=0.0005, t=3.567, Df=171) while the total herbivores hade a negative significant response to plant diversity (P=0.0477, t=1.994, Df=171). Both the predator abundance (P=0.00035, t=3.649, Df=169) and the predator diversity (P=0.0245, t=2.27, Df=169) had a positive significant response to plant diversity. The herbivore abundance did not have a significant response to plant diversity but the trend of the response was negative, while the herbivore diversity had a positive significant response to plant diversity (P=0.0285, t=2.209, Df=169). Plant damage showed a negative significant response to plant diversity

(P=0.0033, t=-2.98, Df=171) (**Figure 1**). The trophic level (**model 1**) and response (**model 2**) had a significant response to plant diversity (**Table 2, models 1** and **2**, respectively).

3.2. Specialization (generalists and specialists) response to plant diversity

The specialization showed a significant response to plant diversity (**Table 2**, **model 3**). All generalists (predator and herbivore considered together) responses to plant diversity were positive (P=0.0102, t=2.597) while it was not significant for specialists (P=0.4663, t=0.730). Both generalist predator and herbivore showed a positive significant response to plant diversity (P=0.0275, t=2.224, Df=168; P=0.000457, t=3.575, Df=168 respectively) while it was not significant for specialist herbivores (P=0.100, t=1.652, Df=168). The interaction between the specialization and the response (abundance and diversity) did not have a significant response to plant diversity (**Table 2, model 5**). The interaction of the specialization with trophic level (**Table 2, model 6**), response (**Table 2, model 7**), response and trophic level (**Table 2, model 11**) showed no significant response to plant diversity.

3.3. Effects of scale

The scale showed a significant response to plant diversity (**Table 2**, **model 4**), but specialization influences the scale at which arthropods respond to plant diversity (**Table 2, model 10**). The specialist herbivore diversity was higher with the increasing of spatial scale while the generalist herbivore abundance was lower with the increasing of spatial scale. The trend of generalist predator abundance was not clear (**Figure 2**). The interaction of the scale with the trophic level (**Table 2, model 8**), response (**Table 2, model 9**), trophic level and response (**Table 2, model 12**) showed no significant response to plant diversity.

3.4. Effects of habitat

Habitat showed no significant response to plant diversity (t=-0.07, P=0.945). The predators did not significantly respond to plant diversity in natural (P=0.193, t=-1.13, Df=69), non-crop (P=0.654, t=0.45, Df=69) and crop (P=0.193, t=-1.34, Df=69) habitats but the trend was positive response for the three habitats. The herbivores did not significantly respond to plant diversity in natural (P=0.633, t=0.479, Df=69), non-crop (P=0.900, t=-0.127, Df=95) and crop (P=0.845, t=0.196, Df=95) habitats but

the trend was positive response for crop and negative response for natural and non-crop habitats (**Figure 1**).

4. Discussion

4.1. Effect of plant diversity on predators and herbivores

Our quantitative synthesis of 175 studies on 32 papers showed that a beneficial effect of plant diversity generalist predators. Predators had a strong positive overall response to plant diversity. By definition, plant diversity usually increases the biomass and diversifies habitat structure supporting predators. We can hypothesize that plant diversity participated to increase the abundance of predators by providing more alternate prey (Mollot et al. 2012), nectar sources, and suitable microclimate (Landis et al. 2005). Our conclusions have a good agreement with the meta-analysis of Letourneau 2011 that supported a positive effect of plant diversity of enemies. Interestingly, we showed a similar trend to the one observed at landscape scale (Chaplin-Kramer et al. 2011). Indeed, similarly to this later study, we did not observe a significant response of herbivore abundance to plant diversity. Inversely, this response was significantly negative in the Letourneau et al. (2010) meta-analysis. We can hypothesize that the absence of significant response in our study may be attributed to the fact that there is an inverse effect of plant diversity for specialist herbivores (non-significantly negative) while it is significantly positive for generalist herbivores. This suggest that in the case of generalist herbivores, the regulation of generalist predators might be completely dampen by a strong positive bottom up effect of plant diversity, made possible because of their generalist status. Inversely, for specialist herbivores, the positive bottom-up effect in more diversified systems should be smaller and may not counter-balance the increased control of generalist predators. The similarity of our results with the meta-analysis of Chaplin-Kramer et al. (2011) support the hypothesis that plant diversity effect on arthropods community, and *in fine* on herbivore control, follows similar rules across scales but rather depends on life dispersal history traits of both predators and herbivores (Tscharntke et al. 2007).

4.2. Effects of scale and habitat

While the effects of the scale remain quite fuzzy, there was a trend for an increasing effect of the scale of observation on the response of specialist herbivores, while it was decreasing with the scale

for generalist herbivores (**Figure 2a** and **b**). More precisely, we observed for specialist herbivores a trend for a negative response to plant diversity at lower scale and a trend for a positive response at larger scales. This suggests that at lower scales plant diversification alters habitat effect and predation sufficiently to reduce specialist herbivores. At broader scales, plant diversification seems to have an overall positive effect on specialist herbivore. These results are consistent with the resource concentration hypothesis, indeed specialist herbivores may find more easily an appropriated resource at both broader and smaller scale (Andow 1991), thus mitigating the top-down control of predators. The absence of significant effect of the scale on the response of generalist predators to plant diversification (**Figure 2c**) suggest that either i) the influence of plant diversity occurs at broader scales as showed by Chaplin-Kramer et al. (2011) that showed that the most predictive scaleof response is between 1500 and 2000m, or ii) there is no effect of the scale and the most important scale of organization varies in all studies, probably in relation with the dispersal ability of generalist predators.

Our results showed that there was no significant effect of the habitat (natural, non-crop, and crop) on the response of predators and herbivore to plant diversification. This result suggests that plant diversity had similar effect in all habitats. However, we can notice that plant diversity tends to have a greater negative effect in crop habitat than in non-crop habitat (**Figure 1**). This difference between habitats may be explained by initial plant diversity higher in non-crop habitat compared to crop habitat, thus limiting the effect of additional diversification.

In summary, we confirm that plant diversity alters differently herbivores and predators involved in pest control. The effect of plant diversity differed strongly according to the trophic level, and on the arthropod specialization. The spatial scale seems to have a moderate to no effect on the response of arthropods to plant diversification. Overall, our results suggest that the response of herbivore to plant diversification is a balance between habitat and trophic effect that varies according to arthropod specialization and types of habitats.

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Table 1. List of 32 papers included in meta-analysis, the values are the number of each predicted variable (abundance, diversity and plant damage) studied for predators and herbivores in the papers.

	Predators		Herbivores		Plant
Authors of papers	**Abundance**	**Diversity**	**Abundance**	**Diversity**	**damage**
Bickerton and Hamilton 2012	3		2		
Brose 2003		1			
Cruz et al 2013	1	1			
Diehl et al. 2013		1		2	
Fabian et al. 2014	1		1		
Fernandes et al 2013			2		
Gámez-Virués et al 2010	1		1		
Haddad et al. 2009	1	1	3	1	
Haddad et al. 2011	1	1	1	1	
HansPetersen et al 2010	14		28		
Hummel et al 2012	3	1			
Lin et al 2003	2		1		
Lin et al 2011			2		
Nakahira et al 2012	1		2		
Nemec et al. 2014	2				
Noman et al. 2013	1		1		
Nyasani et al 2012	4		18		
Pitan and Odebiyi 2001			4		1
Ramalho et al 2012	1		3		
Sobek et al 2009	1		1		
Song et al 2013	5		1		
Srinivasa Rao et al. 2012	3		4		
Staudacher et al. 2013			1		1
Stenchly et al 2012	1	1			
Straub et al. 2013	1		3		1
Straub et al. 2014	2		1		1
Tulli et al. 2013	1		1		
Wang et al 2011	2		2		
Yang et al 2012	6		3		
Yao et al 2012	2		8		
Zhou et al 2013a	2		1		
Zhou et al. 2013b	1		2		
Responses	**63**	**7**	**97**	**4**	**4**
Studies	**26**	**7**	**26**	**3**	**4**

Table 2. Models tested for study questions, the effect of predictor variables

Model	Predictor variables	Response variable	Papers and Observations	Df	Residual deviance	Pvalue (>|F|)
1	Trophic level	effect size	32, 172	2	79.59	<0.00001
2	Response	effect size	32, 173	2	94.18	0.04147
3	Specialization	effect size	32, 173	2	87.967	<0.00001
4	Scale	effect size	32, 162	1	94.839	0.02309
5	Trophic level x response	effect size	32, 170	1	78.407	0.1138
6	Trophic level x Specialization	effect size	32, 169	1	78.493	0.9359
7	Response x specialization	effect size	32, 169	1	86.353	0.3753
8	Trophic level x scale	effect size	32, 169	2	78.631	0.4841
9	Response x scale	effect size	32, 170	2	91.495	0.80591
10	Specialization x scale	effect size	32, 170	2	81.694	0.007953
11	Trophic level x response x specialization	effect size	32, 165	1	76.980	0.6587
12	Trophic level x response x scale	effect size	32, 165	1	77.343	0.8429

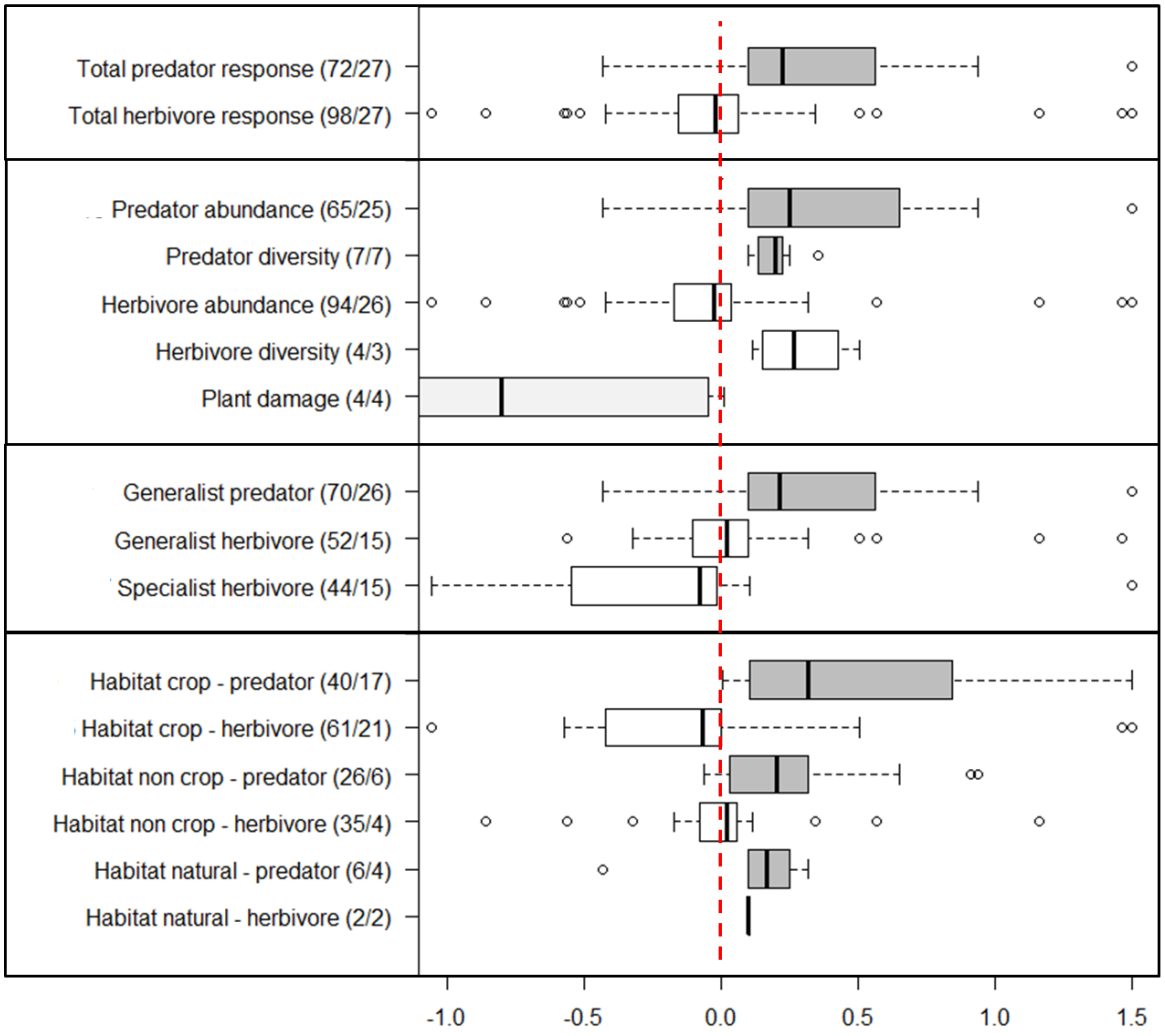

Figure1. Arthropod responses to plant diversity, based on 32 studies and 175 total responses. Numbers in parentheses denote total number of responses/total number of studies, respectively. The predators, herbivores and damage are in grey, white, and light grey respectively.

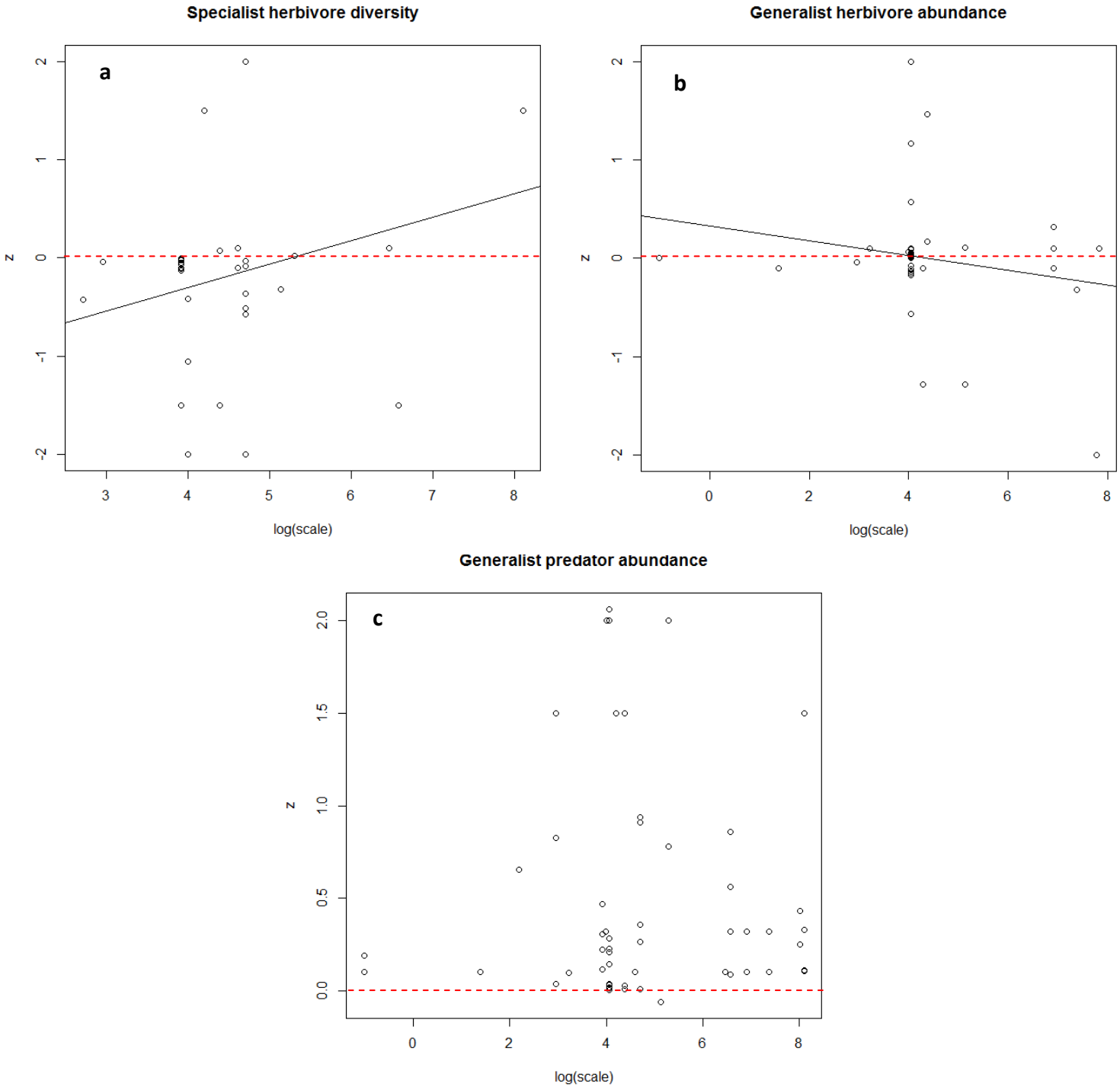

Figure 2. Effect of the scale of observation (log scale in m) on the response of arthropods to plant diversity; for specialist herbivore diversity (a), generalist herbivore abundance (b), and generalist predator abundance (c).

Chapitre 2. En conditions paysannes, comment la diversité végétale affecte la structure de la communauté des arthropodes?

Ce chapitre vise à comprendre comment la diversité des plantes structure les réseaux trophiques des arthropodes dans les systèmes multi-espèces à base de plantain. Il s'agissait d'une caractérisation de la communauté des végétaux et celle des arthropodes. Ce chapitre repose sur deux articles dont le premier soumis à Basic and Applied Ecology et est intitulé **<Contrasting effect of plant diversity across arthropods trophic groups and spatial extends: case of multi-specific plantain based agroecosystems>**. Le second article traite des interactions entre les communautés des fourmis dans les agroécosystèmes de plantain et est intitulé **<Cultivated plant diversity and interspecific interactions drive the assemblage of the ant community in diversified plantain-based agroecosystems>.** Ce deuxième article est soumis à Journal of Applied Ecology.

L'objectif principal de ce chapitre était de décrire la structure des réseaux trophiques des arthropodes dans un réseau de 20 parcelles en milieu paysan. Ces parcelles se situent aux alentours du Centre Africain de Recherches sur Bananiers et Plantains (CARBAP) à Njombé dans le département de Moungo au Cameroun. Il existe dans ces systèmes une gamme de diversité de cultures associées permettant d'aborder la question de la diversification végétale sur la communauté des arthropodes. La caractérisation de la communauté végétale a été faite par la prise des coordonnées géographiques de chaque plante et la détermination de la diversité végétale sur chaque parcelle.

Nous avons ensuite caractérisé la communauté des arthropodes par des mesures d'abondance avec piégeage régulier en utilisant des pièges attractifs avec appâts pour capturer les taxa de fourmis et des pièges à pseudo-troncs de bananier pour capturer les autres taxa d'arthropodes présent au sol et dans la litière. Le piégeage a permis de décrire la communauté des arthropodes. Nous avons effectué les analyses isotopiques des plantes et des arthropodes et nous nous sommes basés sur les signatures isotopiques en carbone et azote pour faire une simplification en groupes trophiques homogènes de la communauté des arthropodes. Ensuite nous avons cherché à comprendre la relation entre la diversité des plantes et l'abondance des groupes d'arthropodes à l'échelle du quadrat et de la parcelle.

Contrasting effect of plant diversity across arthropods trophic groups and spatial extends: case of multi-specific plantain based agroecosystems

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Abstract

Previous biodiversity studies have shown that plant diversity has positive effects on arthropod food web structure. However, only few studies addressed this issue in tropical ecosystems while they have fewer annual variations, allowing the community to tend a steady state. With the goal of optimizing pest management, we studied the effect of plant diversity on the arthropod community at three spatial scales (5.8, 51.8, and 144 m^2) in 20 plantain-based fields in Cameroon. Plantain-based agroecosystems are especially useful for studying the effects of plant diversity because they contain few to many non-plantain crop plants, a variety of spatial organizations, and few or no inputs of pesticide or fertilizer. We measured the diversity of cropped plants and the abundance of ground-dwelling arthropods. Five trophic groups of arthropods were identified based on stable isotopic signatures ($\delta^{13}C$ and $\delta^{15}N$). At a scale of 144 m^2, predator abundance was positively correlated with plant diversity while herbivore abundance was negatively correlated with plant diversity. This strong and inverse effect of plant diversity on herbivore and predator abundance suggests that top-down forces and resource concentration structure the arthropod community in plantain fields. Our findings are also consistent with other studies that showed a reduction of interaction and interference between predators in more structured habitats. We also found that the scale at which plant diversity alters the abundance of arthropods differs depending on the arthropod trophic group and taxon. These findings will help in the design of plantain agroecosystems that enhance pest control services.

Keywords: Arthropod food webs, Plot scale, Multitrophic interactions, Habitat structure, Cameroon

1. Introduction

Functional diversity and associated biodiversity in agroecosystems provide and promote important services to human society such as pollination, biological control, and nutrient cycling (Costanza, dArge, deGroot, Farber, Grasso et al. 1997). Substantial research has shown that a loss of biodiversity usually alters ecosystem functioning (Kruess & Tscharntke 1994) and may have critical consequences for sustainable food production and carbon sequestration. The effect of biodiversity on ecosystem characteristics, including belowground biomass, pollination, and predation and parasitism of pests, is mediated by the heterogeneity of resources and their spatial organization (Tylianakis, Rand, Kahmen, Klein, Buchmann et al. 2008). Currently, there is a critical need to better understand the effect of plant diversity and its spatial arrangement on the functioning of agroecosystems so as to enhance production while maintaining ecosystem services.

Plant diversity determines the structure of food webs (Eisenhauer, Dobies, Cesarz, Hobbie, Meyer et al. 2013; Haddad, Crutsinger, Gross, Haarstad & Tilman 2011) and affects the abundance, diversity, and functioning of species at higher trophic levels (Ebeling, Klein, Weisser & Tscharntke 2012; Loranger, Weisser, Ebeling, Eggers, De Luca et al. 2014; Unsicker, Baer, Kahmen, Wagner, Buchmann et al. 2006). Scherber et al. (2010) recently documented a positive effect of plant diversity on the abundance and diversity of most trophic groups (except invasive groups), and this effect decreased from lower to higher trophic levels. As a result, ecosystems with higher plant diversity usually support increased levels of pest regulation (Letourneau, Armbrecht, Rivera, Lerma, Carmona et al. 2011; Quijas, Schmid & Balvanera 2010).

In agroecosystems, plant diversity helps to sustain insect and natural enemy populations and often supports increased levels of pest predation (Landis et al. 2005). The review of Andow (1991) have showed the role of vegetation diversity in integrated pest management emphasizing biological control interactions among insect pests, natural enemies and other crop pests. Habitats favored in plant-diversified system enhance the populations of natural enemies (Tylianakis, Tscharntke & Lewis 2007). Pests can be controlled by both bottom-up effects from plants and by top-down effects by natural enemies (Rosenheim 1998). Theories suggest that plant diversity enhances pest control by stabilizing natural enemy communities (Tylianakis & Romo 2010) and by providing resources that have indirect effects on higher trophic levels through bottom-up trophic cascades (Power 1992). The meta-analyses (Bommarco & Banks 2003; Hambäck & Englund 2005; Tonhasca & Byrne 1994) have

demonstrated that diversified crops and host plant size (Bach 1988) tend to reduce density of herbivores by the hypothesis of resource concentration and enemies. In agroecosystems, plant diversity may be manipulated directly in the cropped field (Landis, Wratten & Gurr 2000) or in neighbouring habitats including field margins (Denys & Tscharntke 2002), diversity strips, (Moonen & Marshall 2001; Thomas & Marshall 1999), or hedgerows (Zuria, Gates & Castellanos 2007).

The effect of diversity on the biological regulation of populations is strongly altered by its spatial heterogeneity (Tylianakis et al. 2008). In a recent meta-analysis, the effect of landscape complexity (diversity of land uses) on natural enemy abundance was positive but the effect on pests was unclear (Chaplin-Kramer, Megan, Rourke, Eleanor & Kremen 2011). This study also showed a stronger effect of landscape complexity on specialist enemies than on generalist enemies at a local scale (see Figure 3a in Chaplin-Kramer et al. 2011). While an increasing number of studies have considered both plant diversity and spatial arrangement at the landscape scale (Crist, Pradhan-Devare & Summerville 2006; Tscharntke, Steffan-Dewenter, Kruess & Thies 2002), similar studies at a local scale remain scare (Perfecto & Vandermeer 2008). The local scale, however, is the primary scale of management for farmers. This lack of study is perhaps the result of the great simplicity of spatial organisation and plant diversity at the local scale, especially in temperate cropping systems, but future sustainable systems will probably exhibit higher levels of complexity at all scales (Malézieux 2012; Malezieux, Crozat, Dupraz, Laurans, Makowski et al. 2009). Tropical systems often exhibit a much greater complexity (for both plant diversity and spatial complexity) than temperate systems. Tropical systems may therefore be useful for studying the effect of plant diversity and its spatial complexity on the structure of arthropod food webs and on pest regulation.

In African humid tropics, plantains (cooking bananas with *Musa* AAB genome) are cropped in association with annual crops (roots, tuber, and vegetable crops) and perennial crops (cocoa, coffee, palm, and others) crops. Plantain fields may be planted with > 20 kinds of other crop plants. These systems are mainly grown with few or no inputs of fertilizer or pesticide. In most banana and plantain production areas, the most important pest is the banana weevil, *Cosmopolites sordidus* (Coleoptera: Curculionidae) (Germar. 1825) (Gold, Pena & Karamura 2001). *Cosmopolites sordidus* is a narrowly oligophagous pest, attacking wild and cultivated clones in the related genera *Musa* (banana, plantain, and abaca) and *Ensete* (Gold et al. 2001). Natural control by generalist predators, e.g. Dermaptera, Staphylinids, Histerids, Formicids, represents the most appropriate way to manage this pest (Abera-Kalibata, Hasyim, Gold & Driesche 2006).

In a simple banana agroecosystem, Duyck et al. (2011) showed that the addition of a primary resource (a cover crop) alters the structure of the arthropod community. In another study, addition of a cover crop also increased the abundance of *Solenopsis geminata* (Myrmicinae), a potential predator of *C. sordidus*, and the predation of *C. sordidus* eggs artificially placed on banana plants (Mollot, Tixier, Lescourret, Quilici & Duyck 2012). We suspect that the presence of multiple crops should also change the structure of arthropod food webs in plantain systems. In contrast to the cover crops in simple banana fields, which typically have a homogeneous distribution, the various crops in plantain fields usually have a heterogeneous distribution.

Given that management of plant diversity is the primary pest management choice of small-scale plantain and banana farmers, it is important to understand how plant diversity can influence the structure of arthropod food webs and the control of *C. sordidus*. It is particularly important to quantify the effect of plant diversity, to identify the crops that are altering food web structure, and to understand at which scale these processes are occurring.

In the research described in this paper, we studied the effect of plant diversity on the arthropod community in plantain-based, multi-species agroecosystems in Cameroon. We described the structure of arthropod food webs in 20 farmer fields. Based on $\delta^{13}C$ and $\delta^{15}N$ isotopic signatures, we identify arthropod trophic groups, i.e., arthropods that share the same food resources and consumers. We determined whether the abundance of different arthropod taxa and trophic groups can be correlated with plot-scale plant diversity. Then, we investigated at which scale (quadrat = 5.76 m², neighbouring quadrats = 51.84 m², or plot = 144 m²) plant diversity alters the abundance of arthropod trophic groups and arthropod taxa. Finally, we discussed the significance of the plant diversity effect with regard to food web structure and the control of herbivorous arthropods.

2. Materials and methods

2.1. Study sites

The study was conducted in the Moungo department of the Littoral Region of Cameroun (Central Africa) from June 2012 to February 2013. We selected 20 farmer fields near the CARBAP Research Station (4° 34’ 11.33’’ N; 9° 38’ 48.96’’ E; 79 m a.s.l.); the environmental conditions are similar for all of the fields, which have a young brown soil derived from a volcanic platform (Delvaux, Herbillon & Vielvoye 1989). The climate is humid tropical with a monthly mean temperature ranging from 25.0 to 27.4°C and a mean annual rainfall of 2610 mm. All fields contained plantain crops (*Musa AAB* genome) and a diverse array of other annual and perennial crops. In selecting these fields, we

explored the existing diversity of plantain-based agroecosystems rather than the controlled diversity of experimental fields. Pesticides and fertilizers are rarely applied in these extensively managed systems.

2.2. Identification and enumeration of plants and arthropods

In each field, we determined the abundance of each arthropod taxon and plant species during two periods: the rainy season (mid-March 2012 to mid-November 2012) and the dry-season (mid-November 2012 to February 2013). In each field, all determinations were conducted in one 12 X 12 m plot that was subdivided into 25 quadrats of 2.4 X 2.4 m. In each quadrat, we identified all crop plants, and measured their coordinates with a measuring tape (using quadrat corners as the reference to minimize error). To measure the diversity and abundance of arthropods, we successively used two types of traps placed in the centre of each quadrat. First, we used an attractive trap composed of 30 X 30 cm white ceramic plates, each of which had at its centre a 4-cm spot of bait composed of honey mixed with canned tuna. This first type of trap (the bait trap), which was designed to detect the diversity and abundance of ants, was deployed for 30 minutes before ants were collected with an aspirator. Ants were counted in digital photographs of the samples. Just after the bait trap was removed, we deployed one banana stem trap (made of one-half of a 20-cm-long segment of plantain stem) in the same position to capture other arthropods. After 48 h, arthropods on and near the stem traps were collected with an aspirator. All samples of both traps were kept for taxonomic description in the laboratory and were frozen for isotopic analysis. Ants were identified with the aid of the Bolton key (Bolton 1973) and the PIAkey (Sarnat 2008). Other arthropods were identified with the aid of two books (Lavabre 1992). Overall, we determined the location of 8325 plants belonging to 31 species **(Table S1)** and captured 19946 ants belonging to 14 species with bait traps and 1730 arthropods belonging to 19 species with banana stem traps. We retained for further analysis the arthropods that were present in at least three fields with a total abundance in each field > 6 individuals; these criteria were met by 15 species of arthropods (**Table 1**).

2.3. Isotopic analyses

There was uncertainties on the trophic level of many collected taxa. The isotopic analysis allowed to determinate the trophic group of each taxa and to constitute constitute homogeneous trophic groups. Changes in a consumer's diet may be indicated by changes in the isotopic signatures of ^{13}C

and ^{15}N (Oelbermann & Scheu 2002; Ponsard & Arditi 2000; Vanderklift & Ponsard 2003). The ^{13}C signature of plants differs depending on whether they have C3 or C4 photosynthetic metabolism. The ^{13}C signature of consumers indicates the origin of the carbon of the primary resources that they consumed. Regular enrichment of ^{15}N along trophic chains allows researchers to use an organism's ^{15}N signature to estimate its trophic level. The simultaneous use of ^{13}C and ^{15}N signatures enables determining an organism's trophic niche, i.e., the primary producer that directly or indirectly provides its carbon source and its trophic level.

After sampled arthropods were taxonomically described, all were lyophilized for 48 h and then ground into a fine powder before a 1-mg sample of the powder was placed in a tin capsule for analysis. For each of the 15 arthropod taxa that were identified and kept for analyses, we measured one pooled sample per plot, leading to 300 samples. Isotope ratios were determined with an isotope ratio mass spectrometer EA2000 (Eurovector) coupled to an Isoprime mass spectrometer (elemental analyser) at the Biochemistry and Plant Molecular Physiology Laboratory of the Integrative Biology Institute for Plants (IBIP) at SupAgro-INRA of Montpellier-France. All stable isotope values are reported in the δ notation, with $\delta^{13}C$ or $\delta^{15}N$ calculated as $[(R_{sample} / R_{standard}) - 1] \times 1000$, where R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Standards were PeeDee Belemnite (Peterson & Fry 1987) and atmospheric air (Mariotti 1983) for C and N, respectively.

2.4. Data processing

We defined five trophic groups of arthropods based on their mean $\delta^{13}C$ and $\delta^{15}N$ values using the 'hclust' function from the package 'cluster' version 1.14.1 (Maechler 2013) in R version 2.14 (R Development Core Team 2012). The abundance of each trophic group was calculated by summing the abundance of arthropods belonging to the group. Plant diversity was assessed for each quadrat (5.76 m²), group of 3 X 3 quadrats (nine neighbouring quadrats, 51.84 m²), and plots (25 quadrats, 144 m²) with the Shannon Index (Shannon 1948), which was calculated with the 'diversity' function of the 'vegan' package, version 1.16.32 (Dixon 2003).

2.5. Statistical analysis

First, we analysed the effect of plant diversity on the abundance of arthropod species and trophic groups at the plot scale by considering the whole-plot plant diversity and arthropod abundance (sum of the capture of the 25 traps of each plot, **Figure 1a**). Then we tested the effect of plant diversity at

increasing scales (quadrat, neighbouring quadrats, and plot; **Figure 1b, c, and d**) on the abundance of arthropod trophic groups measured at the quadrat scale.

Generalized linear mixed-effects models (GLMM, Bolker et al., 2009) with a Poisson error were used to examine the relationship between plant diversity and arthropod abundance. In this type of model, the linear predictor contains random effects in addition to fixed effects. We treated 'plot' as a random effect to account for pseudo-replication and because we assumed that plots contained unobserved heterogeneity that we could not model. The GLMMs were fitted by the Laplace approximation using the 'glmer' function in the 'lme4' package (Bates, Maechler & Bolker 2011). We built GLMMs by the standard reduction method; at each step, the significance of each term was assessed by comparing models with and without that term. ΔAIC (difference in Akaike information criterion) was used to assess the difference between each model and the best model.

3. Results

3.1. Effect of plant diversity at the plot scale on the abundance of arthropod taxa and trophic groups

Determination of trophic groups

The isotopic signatures of arthropods ranged from -15 to -35 ‰ for $\delta^{13}C$ and from 0 to 25 ‰ for $\delta^{15}N$. Clustering based on $\delta^{13}C$ and $\delta^{15}N$ led to the definition of five trophic groups (**Figure 2, Table 1**). Trophic group 1 had high isotopic signatures for $\delta^{15}N$ (the mean values for species ranged from 13 to 14 ‰) and included generalist predators in the *Dermaptera* and *Araneae*. Trophic group 2, whose isotopic signatures of $\delta^{15}N$ ranged from 5 to 8 ‰ for species means, included herbivorous and detitrivorous taxa (*Rhinocricidae*, *Metamasius hemipterus*, *Tenebrio sp.*, and *Termitidae*). Trophic group 3, which had an isotopic signature for $\delta^{15}N$ of 5 ‰ for species means, included only *C. sordidus*. Trophic group 4, which had isotopic signatures for $\delta^{15}N$ ranging from 9 and 10 ‰ for species means, included the herbivores *Gryllus* spp. and *Porcellionidae*. Trophic group 5, which had isotopic signatures for $\delta^{15}N$ ranging from 8 and 13 ‰ for species mean, included the omnivorous ants *Monomorium bicolor*, *Monomorium* sp., *Odontomachus mayi*, *Pheidole megacephalla*, *Pheidole* sp., *Paratrechina longicornis*, *Camponotus acvapimensis*, and *Camponotus brutus*.

Relationship between plant diversity and the abundance of taxa and trophic groups at the plot scale

Plant diversity was positively related to the abundance of *Camponotus acvapimensis*, *Metamasius hemipterus*, and *Dermaptera* and was negatively related to the abundance of *Porcellionidae*, *Rhinocricidae*, *Paratrechina longicornis*, *Pheidole* sp., and *Termitidae* (**Table 3, Figure 3**). The relationship between plant diversity and abundance was nearly significant for *C. sordidus* and was insignificant for *Araneae*, *Gryllus* sp., *Monomorium* sp., *Odontomachus mayi*, *Pheidole megacephalla*, or *Tenebrio* sp. (**Table 3**). Plant diversity was significantly associated with the abundances of trophic groups 1, 2, and 5. The relationship was nearly significant for trophic group 3 but was not significant for trophic group 4 (**Table 2**). Plant diversity was positively related to the abundance of trophic group 1 but was negatively related to the abundances of trophic groups 2 and 5 (**Figure 4**).

3.2. Relationship between plant diversity and the abundance of arthropod trophic groups and taxa at increasing scales

Globally, plant diversity was not significantly related to arthropod abundance at quadrat and plot scales but significantly related only at neighbouring quadrats scale (**Table 4**).The relationship between plant diversity and the abundance of arthropod trophic groups differed depending on the group and on the scale at which plant diversity was considered. Plant diversity was positively related to the abundance of generalist predators (trophic group 1) at the plot scale and was positively related to the abundance of herbivores (trophic group 4) at the quadrat and neighbouring quadrats scale (**Table 5**). In contrast, plant diversity was negatively related to the abundance of herbivores/detritivores (trophic group 2) but there was not significantly related to *C. sordidus (*trophic groups 3) at all scales. For group 2, the variation of AIC increased from the quadrat to the plot scale. Omnivore abundance (trophic group 5) was negatively related to plant diversity at all scales. The relationship between plant diversity and the abundance of arthropod taxa also differed depending on the taxon and the scale (**Table 5**).

4. Discussion

4.1. Relationship between plant diversity and the abundance of arthropod taxa and trophic groups at the plot scale

Indeed, our results show that the abundances of the herbivore and omnivore trophic groups were negatively correlated with plant diversity, while the abundance of the predator trophic group was positively correlated with plant diversity. Another study reported similar results for predator and herbivore abundance (Haddad, Crutsinger, Gross, Haarstad, Knops et al. 2009) but with a weaker

negative effect of plant diversity on herbivores. The reduction in herbivore numbers with increasing plant diversity could result from a stabilization of the food web, allowing an increase and stabilization of predator abundance, as suggested by Ebeling et al. (2012). The increase in predators with plant diversity in the current study could be explained in part by a decrease in interaction and interference between predators, i.e., by a reduction in intraguild predation (Finke & Denno 2002, 2006).

Although theory predicts that trophic cascades are most likely to occur in less diverse systems (Polis & Strong 1996) others effects need to be considered (Polis, Sears, Huxel, Strong & Maron 2000). Indeed, two other factors that could have influenced our results are the direct effects of plant diversity on herbivore and predator abundance. Because herbivores often depend on specific plant hosts as food sources, herbivore numbers could decline with increasing plant diversity simply because the percentage of preferred plant hosts in the community decreases as plant diversity increases. Moreover, in poly-cultures, plant diversity increases the herbivore movement (Straub, Simasek, Dohm, Gapinski, Aikens et al. 2014) probably increasing their vulnerability to predation (Root 1973). Predators, in contrast, may directly benefit from increased plant diversity because an increase in plant diversity may result in an increase in favorable habitats.

To assess the relative importance of the change in the basal food resource vs. the change in habitat with change in plant diversity, laboratory experiments can be very useful (Kalinkat, Brose & Rall 2013). Although the non-experimental nature of the current study does not enable us to assess these various effects of plant diversity on herbivore and predator abundance, the low predator abundance that accompanies low plant diversity seems likely to reduce the regulation of herbivore populations. From a practical perspective, the results indicate that plant diversity in plantain fields helps control plantain pests.

While our results are consistent with some experiments that show strong top-down and cascading effects of predators (Dyer & Letourneau 2003), our results also differ from those of other biodiversity experiments. For instance, Scherber et al. (2010) showed that plant diversity had a positive effect on the abundance of most trophic groups and that this effect tended to decrease with trophic level, suggesting that bottom-up effects controlled the community. Similarly, the recent grassland biodiversity experiment of Rzanny et al. (2013) showed that the composition of the arthropod community was mainly determined by plant-mediated, bottom-up forces. In contrast to our tropical study, however, the latter two studies were conducted in temperate regions. Whereas a tropical climate is relatively stable and therefore supports a relatively stable community, a temperate climate induces an annual collapse in the abundance of all taxa. We argue that the relatively stable

conditions in the plantain-based systems of the current study (these systems were at least 5 years old) allowed top-down forces to structure the community.

4.2. The effect of scale on the relationship between plant diversity and arthropod abundance

We generally found that the effect of plant diversity on the abundance of trophic groups was stronger at the neighbourhood scale than at the smaller (quadrat) or larger (plot) scale, suggesting that there is an optimal scale at which plant diversity affects arthropod abundance. Interestingly, the sign and the magnitude of the effect and the scale that supported the greatest effect differed among trophic groups and arthropod taxa. Predators were strongly and positively correlated with field-scale plant diversity while herbivores and detritivores (trophic groups 2 and 3) were negatively correlated with plant diversity at all scales. Other herbivores (trophic group 4) were positively correlated with plant diversity at quadrat and neighbourhood scales but not at the plot scale. We hypothesize that the scale at which plant diversity affects arthropod abundance can be linked to the dispersal ability and mobility of these organisms. Indeed, predators (e.g., Araneae and Dermaptera) have greater capacities of dispersion and are more mobile than herbivores such as *C. sordidus* (Vinatier, Chailleux, Duyck, Salmon, Lescourret et al. 2010).

That we detected an effect of plant diversity despite the relatively small scale at which plants and arthropods were measured in the current study may be explained by the moderate dispersal capacities of the ground-dwelling taxa in plantain fields. On the other hand, studies with bees, which are able to travel long distances, have also documented significant effects of local plant diversity (Tylianakis, Klein, Lozada & Tscharntke 2006). Understanding how the effects of plant diversity on arthropod abundance are altered by scale is important for pest management because it provides clues as to where to locate plants to maximize the abundance of desirable trophic groups or taxa. In agreement with Stenchly et al. (2011), we emphasize the need for multi-scale management of agroecosystems to improve the conservation of species or trophic groups of interest.

In conclusion, the effect of plant diversity on arthropod abundance in tropical, plantain-based ecosystems differed depending on trophic group and spatial scale. Consistent with results from temperate studies, we documented that plant diversity tended to increase the abundance of predators and reduce the abundance of lower trophic groups. Our results suggest that both habitat and trophic effects structure the arthropod community. Determining which of these two explanations is correct or more correct will require additional research. Understanding the scale at

which plant diversity most affects a given trophic group will help crop managers design agroecosystems that maximize pest regulation.

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Table 1. Systematic classification of the most abundant arthropod taxa identified in 20 plantain-based cropping systems in Cameroon. (* not identified)

Taxa	Trophic group	Class	Order	Family	Genre	Species
Araneae	1	Arachnida	Araneae	*	*	
Dermaptera	1	Insecta	Dermaptera	*	*	*
Metamasius hemipterus	2	Insecta	Coleoptera	Curculionidae	*Metamasius*	*hemipterus*
Rhinocricidae	2	Myriapoda	Spirobolida	Rhinocricidae	*	*
Tenebrio sp.	2	Insecta	Coleoptera	Tenebrionidae	*Tenebrio*	sp.
Termitidae	2	Insecta	Isoptera	Termitidae	*	*
Cosmopolites sordidus	3	Insecta	Coleoptera	Curculionidae	*Cosmopolites*	*sordidus*
Porcellionidae	4	Myriapoda	Isopoda	Porcellionidae	*	*
Gryllus spp.	4	Insecta	Orthoptera	Gryllidae	*Gryllus*	spp.
Camponotus acvapimensis	5	Insecta	Hymenoptera	Formicidae	*Camponotus*	*acvapimensis*
Monomorium sp.	5	Insecta	Hymenoptera	Formicidae	*Monomorium*	sp.
Odontomachus mayi	5	Insecta	Hymenoptera	Formicidae	*Odontomachus*	*mayi*
Paratrechina longicornis	5	Insecta	Hymenoptera	Formicidae	*Paratrechina*	*longicornis*
Pheidole megacephalla	5	Insecta	Hymenoptera	Formicidae	*Pheidole*	*megacephalla*
Pheidole sp.	5	Insecta	Hymenoptera	Formicidae	*Pheidole*	sp.

Table 2. Effect of plant diversity on the abundance of five trophic groups at the plot scale.

Trophic group	Df	AIC	δAIC	logLik	χ^2	Pr(>χ^2)
1	3	77.245	13.631	-35.623	15.631	> 0.0001
2	3	1704.8	246.1	-849.38	248.14	< 0.0001
3	3	210.6	1.38	-102.3	3.3772	0.0661
4	3	64.279	-0.99	-29.139	1.0106	0.3148
5	3	1344.7	86.4	-669.35	88.434	< 0.0001

Table 3. Effect of plant diversity on the abundance of each taxon across 20 plantain fields at the plot scale.

Taxa	Df	AIC	δAIC	logLik	χ^2	Pr(>Chisq)
Araneae	3	66.6	1.5	-30.3	0.52	0.4679
Camponotus acvapimensis	3	557.1	-82.3	-275.5	84.35	< 0.0001
Cosmopolites sordidus	3	210.5	-1.5	-102.2	3.51	0.0606
Metamasius hemipterus	3	150.4	-22.5	-72.2	24.45	< 0.0001
Porcellionidae	3	1098.3	-215.4	-546.1	217.39	< 0.0001
Dermaptera	3	125.3	-26.2	-59.6	28.21	< 0.0001
Gryllus spp.	3	90.1	1.6	-42.1	0.43	0.5114
Rhinocricidae	3	1889.5	-553.4	-941.7	555.45	< 0.0001
Monomorium sp.	3	859.2	1.8	-426.6	0.17	0.6758
Odontomachus mayi	3	144.3	1.4	-69.2	0.59	0.4387
Paratrechina longicornis	3	208.9	-57.5	-101.5	59.46	< 0.0001
Pheidole megacephalla	3	387.9	-0.1	-191.0	2.01	0.1563
Pheidole sp.	3	465.7	-18.0	-229.8	20.01	< 0.0001
Tenebrio sp.	3	90.8	0.2	-42.4	1.79	0.1814
Termitidae	3	209.0	-4.1	-101.5	6.07	0.0137

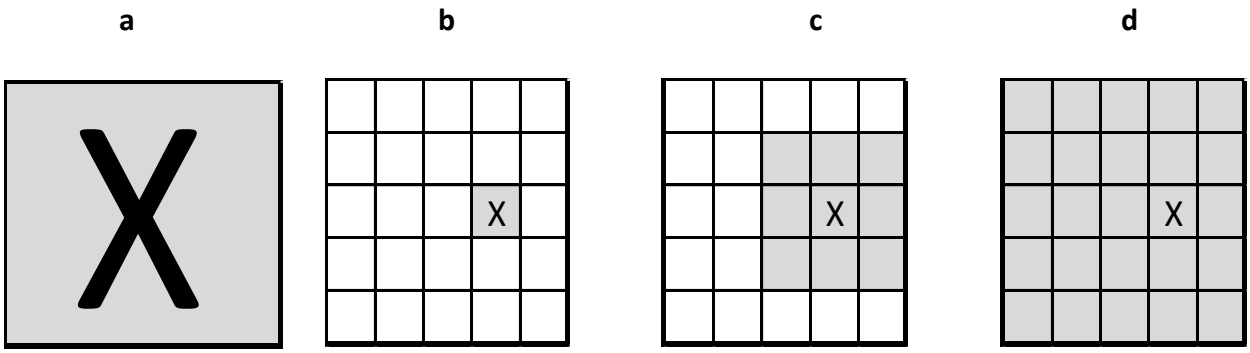
Table 4. Effect of plant diversity on the arthropod abundance depending on the scale at which plant diversity was measured (quadrat, neighbourhood, or plot)

Spatial scales	Df	AIC	δAIC	logLik	Chisq	Pr(>Chisq)
Quadrat scale	11	10413	0	-5195.4	0	1
Neighbourhood scale	11	10274	0	-5126.2	0	< 2.2e-16 ***
Field scale	11	10103	0	-5040.7	0	1

Table 5. Effect of plant diversity on the abundance of arthropods (by trophic group and by taxon) as indicated by variation of the AIC value and depending on the scale at which plant diversity was measured (quadrat, neighbourhood, or plot). The signs after the values indicate whether the slope of the model was positive or negative; a positive or negative sign indicates that abundance increased or decreased, respectively, with plant diversity. NS indicates not significant.

Trophic group / Taxa	**Quadrat**	**Neighbourhood**	**Plot**
GI1	NS	NS	13.6 (+)
GI2	26.6 (-)	106.2 (-)	246.1 (-)
GI3	NS	NS	NS
GI4	6.9 (+)	3.2 (+)	NS
GI5	28.7 (-)	76.3 (-)	86.4 (-)
Araneae	NS	NS	NS
Camponotus acvapimensis	18 (+)	86.6 (+)	83.4 (+)
Cosmopolites sordidus	NS	NS	NS
Metamasius hemipterus	NS	16.8 (+)	23.3 (+)
Porcellionidae	18 (-)	215.1 (-)	215.2 (-)
Dermaptera	NS	17.7 (+)	26.3 (+)
Gryllus spp.	NS	NS	NS
Rhinocricidae	75.6 (-)	300.1 (-)	555.8 (-)
Monomorium sp.	34.1 (-)	1.9 (-)	NS
Odontomachus mayi	NS	NS	NS
Paratrechina longicornis	5.7 (-)	21.5 (-)	58 (-)
Pheidole megacephalla	10 (-)	NS	NS
Pheidole sp.	36 (+)	NS	17.6 (-)
Tenebrio sp.	4.7 (+)	NS	NS
Termitidae	NS	NS	3.7 (-)

Figure 1. Scales used to investigate the relationship between plant diversity and the abundance of arthropod trophic groups or taxa in plantain fields in Cameroon at a) plot scale (144 m^2) analysis of plant diversity on plot scale global arthropods' abundance, and b) quadrat (5.76 m^2), c) neighbourhood (51.84 m^2) and d) plot scales effect of plant diversity on quadrat scale arthropods' abundance.



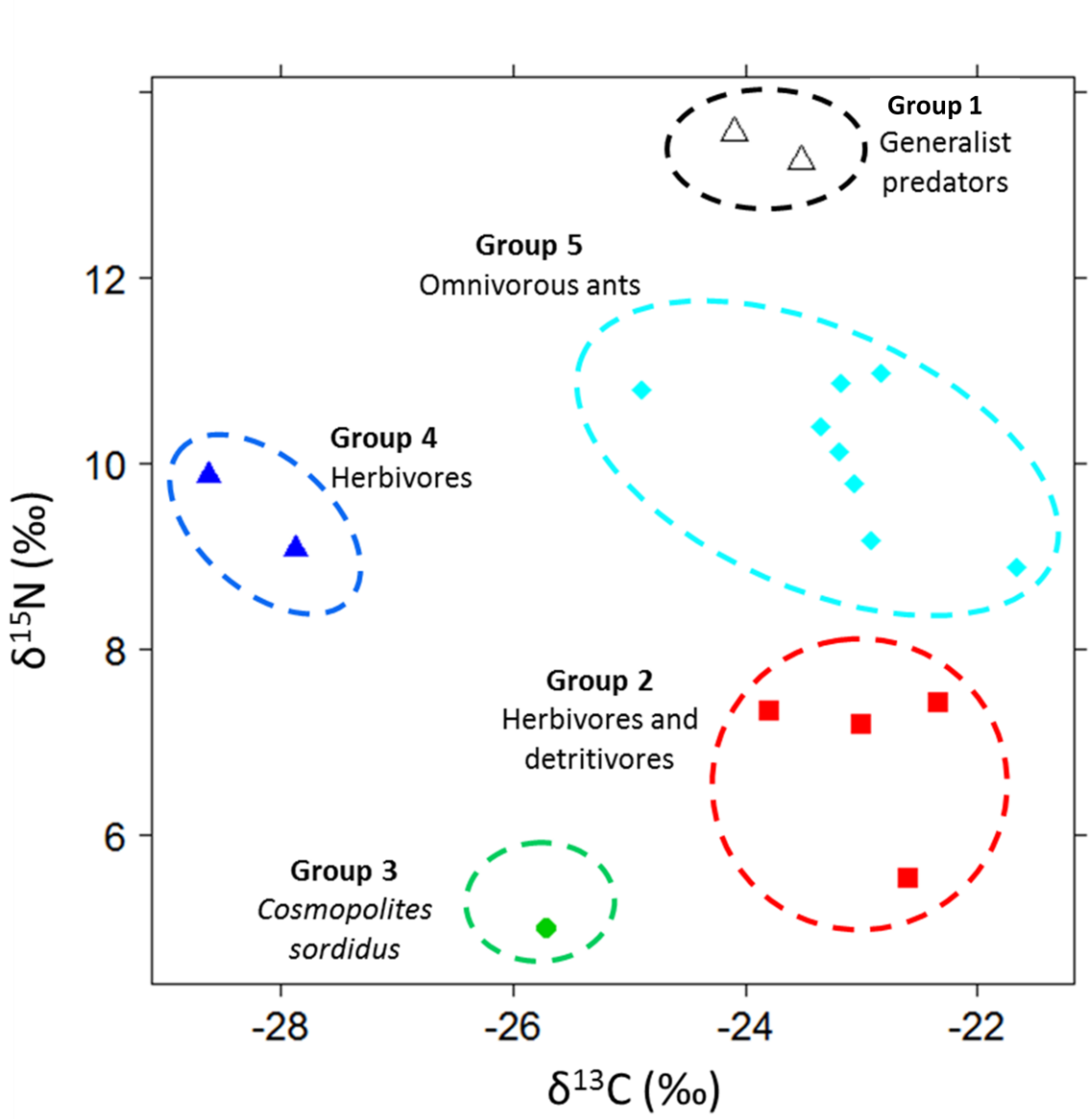


Figure 2. The identification of five arthropod trophic groups based on the mean values of $\delta^{13}C$ and $\delta^{15}N$ signatures of each taxon.

Figure 3. Predicted effect of plant diversity on the abundance of arthropod taxa. Only significant effects are shown. See **Table 3** for details concerning the statistical analysis**.**

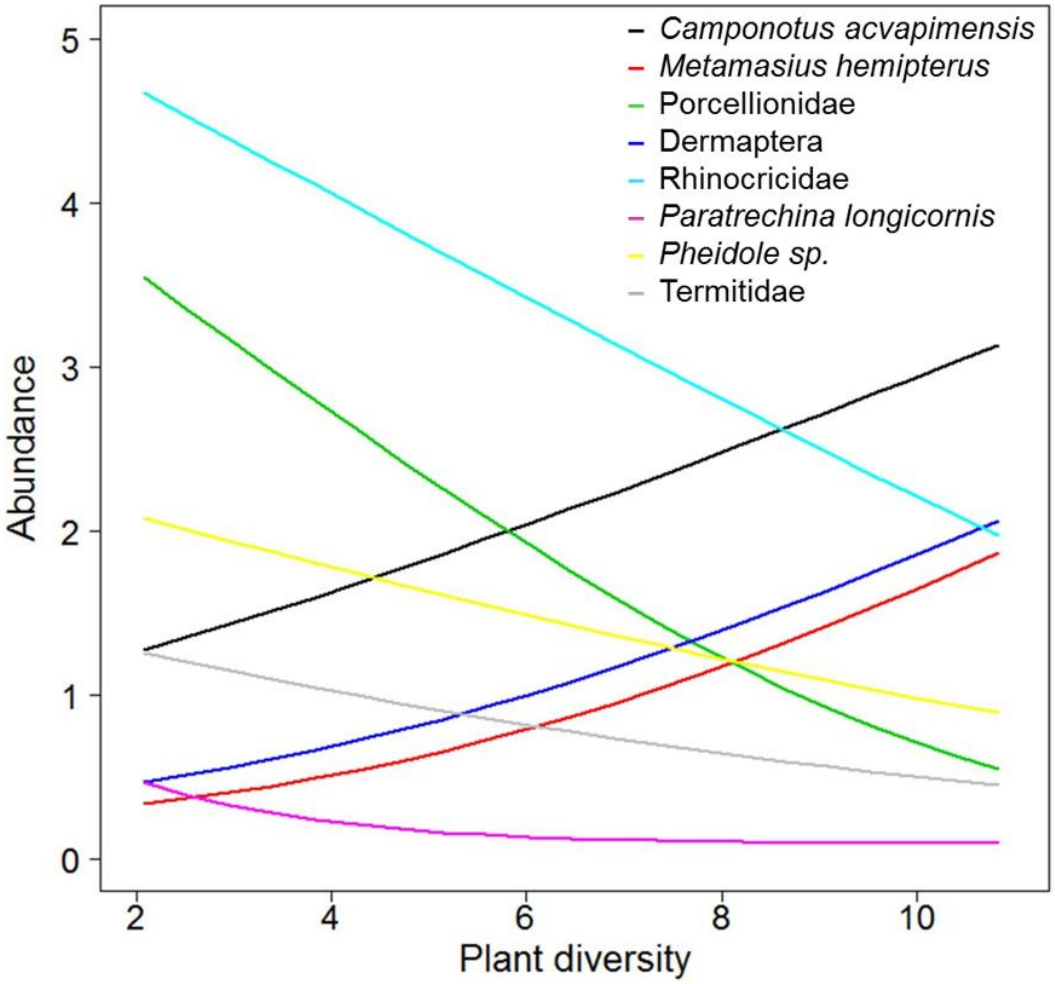
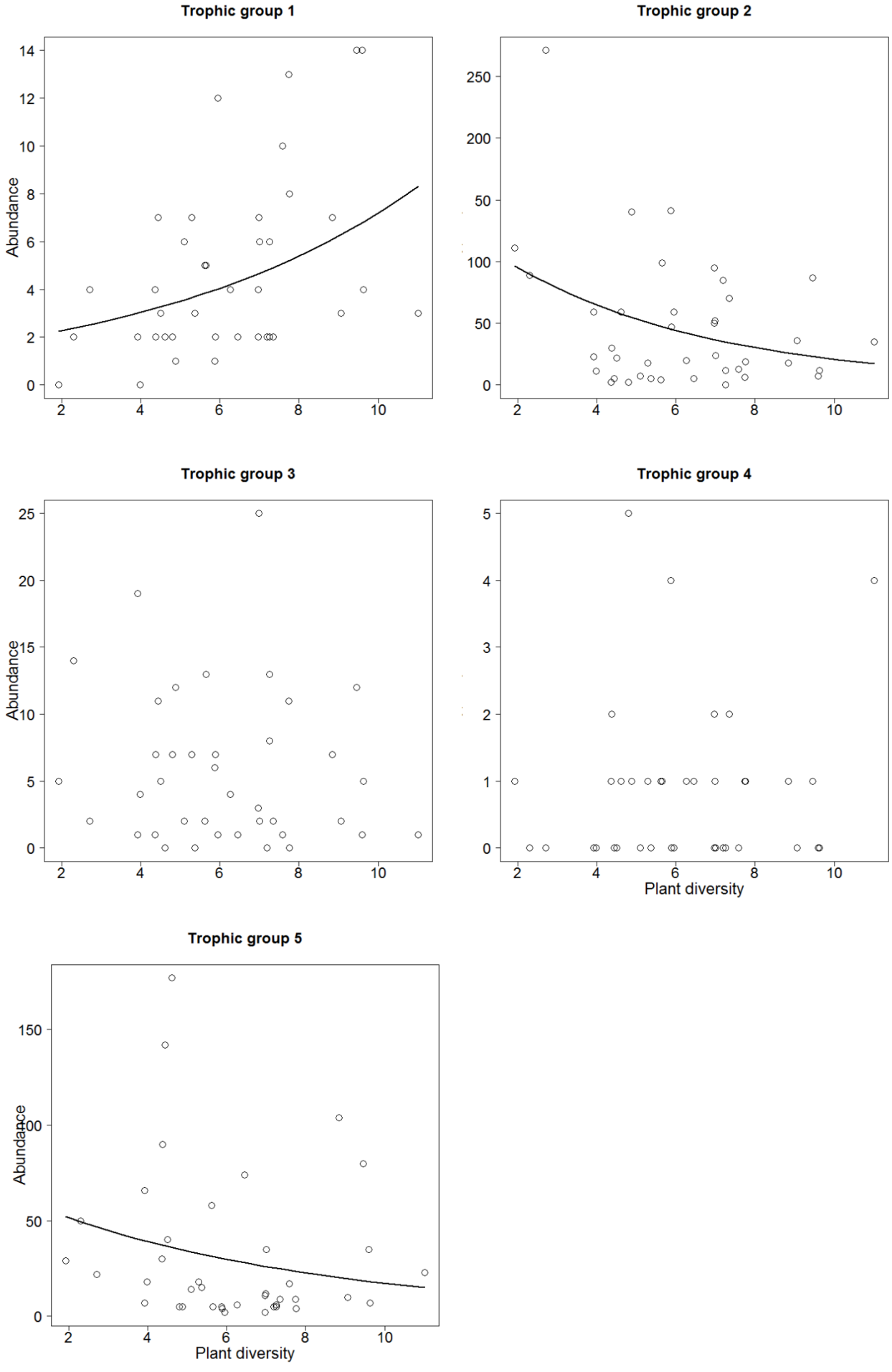


Figure 4. Abundance of trophic groups 1 to 5 as a function of plant diversity measured at the plot scale. Symbols indicate measured abundance, and lines indicate abundance predicted by GLMM when the GLMM analysis was significant. See **Table 2** for details concerning the statistical analysis.



SUPPLEMENTARY MATERIAL

Table S1. Systematic classification of non-plantain crop plants in plantain-based plantain cropping systems in Cameroun.

Taxon	Class	Order	Family	Genus	Species
Amaranthus	Magnoliopsida	Caryophyllales	Chenopodiaceae	*Amarantus*	spp.
Banana	Liliopsida	Zingiberales	Musaceae	*Musa*	*acuminata*
Bitterleaf	Magnoliopsida	Asterales	Asteraceae	*Vernonia*	spp.
Cassava	Magnoliopsida	Euphorbiales	Euphorbiaceae	*Manihot*	*esculenta*
Cocoa	Magnoliopsida	Malvales	Sterculiaceae	*Theobroma*	*cacao*
Cocoyam1 (macabo)	Liliopsida	Arales	Araceae	*Xanthosoma*	*sagittifolium*
Cocoyam2 (taro)	Liliopsida	Arales	Araceae	*Colocasia*	*esculenta*
Cocumber (egussi)	Magnoliopsida	Violales	Cucurbitaceae	*Cucumis*	sp.
Coffee	Magnoliopsida	Rubales	Rubiaceae	*Coffea*	*arabica*
Cola	Magnoliopsida	Malvales	Sterculiaceae	*Cola*	*acuminata*
Cowpea	Magnoliopsida	Fabales	Fabaceae	*Vigna*	*unguiculata*
Crin-crin	Magnoliopsida	Malvales	Tiliaceae	*Corchorus*	spp.
Eru	Gnetopsida	Gnetales	Gnetaceae	*Gnetum*	*africanum*
Garden egg	Magnoliopsida	Solanales	Solanaceae	*Solanum*	*macrocarpon*
Groundnut	Magnoliopsida	Fabales	Fabaceae	*Arachis*	*hypogaea*
Guava	Magnoliopsida	Myrtales	Myrtaceae	*Psidium*	*guajava*
Hot pepper	Magnoliopsida	Solanales	Solanaceae	*Capsicum*	*anuum*
Lime	Magnoliopsida	Sapindales	Rutaceae	*Citrus*	*limon*
Maize	Liliopsida	Cyperales	Poaceae	*Zea*	*mays*
Mango	Magnoliopsida	Sapindales	Anacardiaceae	*Mangifera*	*indica*
Nkui	Magnoliopsida	Malvales	Malvaceae	*Triumphetta*	*pentadra*
Oil palm	Liliopsida	Arecales	Arecaceae	*Elaeis*	*guineensis*
Okra (gombo)	Magnoliopsida	Malvales	Malvaceae	*Abelmoschus*	*esculentus*
Orange	Magnoliopsida	Sapindales	Rutaceae	*Citrus*	*sinensis*
Papaya	Magnoliopsida	Violales	Caricaceae	*Carica*	*papaya*
Pineapple	Liliopsida	Bromeliales	Bromeliaceae	*Ananas*	*comosus*
Plantain	Liliopsida	Zingiberales	Musaceae	*Musa*	*paradisiaca*
Plum	Magnoliopsida	Sapindales	Burseraceae	*Dacryodes*	*edulis*
Sweet patato	Magnoliopsida	Solanales	Convolvulaceae	*Ipomoea*	*batatas*
Tomato	Magnoliopsida	Solanales	Solanaceae	*Solanum*	*lycopersicum*
Yam	Magnoliopsida	Solanales	Dioscoreaceae	*Dioscorea*	spp.

Cultivated plant diversity and interspecific interactions drive the assemblage of the ant community in diversified plantain-based agroecosystems

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Summary

1. By their ubiquity, diversity and abundance, ants are a key component of ecosystems. In tropical ecosystems, ants may represent the major part of animal biomass and are involved in several ecosystem services such as pest regulation. The understanding of mechanisms implied in the structuring of local communities is therefore an important issue in agroecology.
2. In African humid tropics, plantains are cropped in association with highly diversified annual crops and perennial crops. Such agrosystems display a high heterogeneity in vegetation diversity and structure and represent well-suited systems to study how the habitat-related factors and interspecific interactions affect assemblage of ant community.
3. We analyzed here abundance data of six numerically dominant species measured 500 sites among 20 diversified plantain-based fields in Cameroon.
4. We evidenced that the density medium (shrubs) and high (trees) strata of cultivated plants determined the local dominance of species and that plant diversity affects differently the abundance of ant species in the community.
5. We found that interspecific interactions are mostly symmetrically negative but a large variety of interactions are possible between different pairwise species.
6. *Synthesis and application:* Our results indicate that plant diversity and structure may be synergistically used to modulate dominance and abundance of ant species in the composition

of the community at the local scale. Future research in crop management should consider the use of different strata of cultivated plants as a lever to increase resilience of agrosystems and the ecosystem services provided by ants.

Keywords: Vegetation structure, plant diversity, ant community, interspecific interactions, insurance hypothesis, resilience, agrosystem management

Introduction

By their ubiquity, diversity and abundance, ants are a key component of ecosystems. In tropical ecosystems, ants may represent the major part of animal biomass (Hölldobler and Wilson, 1990) and are involved in several ecosystem services such as pest regulation (Perfecto and Vandermeer, 2006; Philpott and Armbrecht, 2006). The understanding of mechanisms implied in the structuring of local communities is therefore an important issue in agroecology. The mechanisms involved in the variations in species diversity, abundances and, consequently, in community structure may be separated into physiological (e.g. moisture) and ecological factors (Philpott and Armbrecht, 2006). The ecological factors can be themselves be distinguished in habitat-related factors (e.g. nesting sites, microhabitats, food availability and diversity) and ecological interactions (e.g. interspecific competition, foraging interference)

Previous studies have shown that vegetation may impact the ant assemblage through the complexity of the habitat structure and the plant diversity (House et al., 2012; Murnen et al., 2013; Perfecto and Vandermeer, 1996; Vasconcelos et al., 2008).In these studies, correlation between habitat-related variation in dominant species incidence and species richness is a general observed trend. Perfecto and Vandermeer (1996) have shown that artificially added shade in tropical agrosystem decreases the abundance of the dominant ant *Solenopsis geminata* whilst it increases the abundance of other species. Vasconcellos et al. (2008) found that the tree and tall grasses covers affect the ant species composition in savannas of South America, with a lower occurrence of the dominant ant species *Solenopsis substitua* in plot with high grass cover. Studying the role of habitat type on abundance and diversity of ant species in an agricultural matrix, House et al. (2012) found that species richness and abundance is higher in native woodland than in pastures or crops, whilst the contrary is observed for dominance by *Dolichoderinae*. In manipulating food and nesting site availability, Murnen et al. (2013) demonstrated that the ant community composition is greatly

influenced by the type of habitat, which reflects the effect of nesting resource availability, whilst the food quantity alone has no effect on community assemblage.

Ant diets vary within and between subfamilies and genera. Many ants may be largely omnivorous and opportunistic, while others are specialized in predation, fungus-growing or in plant consumption (seeds, nectar) (Hölldobler and Wilson, 1990). Therefore, at the community level, ant diets spread on a continuum between herbivorous and strictly predaceous (Bluthgen et al., 2003) and are likely to be affected by plant diversity. Scherber et al. (2010) have shown that plant diversity effects on abundance and species richness dampen with increasing trophic level and degree of omnivory. Blüthgen et al. (2003) proved through isotopes analysis that dominated canopy ant species, with small to intermediate colonies, tend to be largely herbaceous (including extrafloral and floral nectaries), whereas dominant canopy ants, with large colonies, tend to display largely omnivorous diets and understorey or ground-dwelling ants tend to display higher trophic levels.

Habitat-related factors are thus of great importance in ant assemblage but interspecific interactions are another mechanism that drives the assemblage of ant communities. In tropical ant communities, apart from the major guilds of arboreal and terrestrial guilds, which have preferential foraging habitats, some species forage both arboreally and on the ground, connecting the different communities (Blüthgen and Feldhaar, 2010; Dornhaus and Powell, 2010).

Ant species vary, however, in competitive ability due, for example, to foraging activity or colony and body size (Hölldobler and Wilson, 1990). In particular, dominant ants can alter the structure of ant assemblages by interfering in the foraging activity of other ant species (Savolainen and Vepsäläinen, 1988). Dominant ants has often mutualisms with any herbivores which provide honeydew as sugar source in exchange for protection against potential predators (Blüthgen et al., 2004) and allow ants to build large colonies with many nests (Richard et al., 2001). Dominant ants achieve superiority due to their aggressiveness, numerical dominance, superior interference behavior and exploitative competition ability (Parr and Gibb, 2010) and are frequently found in disturbed habitats like intensive agroecosystems (King and Tschinkel, 2006). Therefore, the structure of ant communities is highly affected by variation in the spatio-temporal dynamics of such dominant ants.

The insurance hypothesis of biodiversity function states that differences in the behavior and diet of predators is of importance and may promote long-term stability through complementary functions of predators (Yachi and Loreau, 1999). This is even truer when considering ant communities. As ants diets and resource use spread along a continuum form herbivorous to

predaceous, maintaining ant diversity and abundance is likely to provide a large set of ecosystem services (pollination, pest control) (Rosumek et al., 2009).

In African humid tropics, plantains (*Musa* AAB genome) are cropped in association with annual crops (roots, tuber, and vegetable crops) and perennial crops (cocoa, coffee and palm). Therefore, such agrosystems display a high heterogeneity in vegetation diversity and structure and represent well-suited systems to study how these habitat-related factors and interspecific interactions affect assemblage of ant community. Using diversified plantain agrosystems as model, we assess here (i) the role of vegetation structure on ant dominance; (ii) how diversity and interspecific interactions influence abundance of ant species and (ii) discuss on implication of these ecological factors in agrosystem management.

Materials and Methods

STUDY FIELDS

We conducted in the Moungo department of the Littoral Region of Cameroun (Central Africa) from June 2012 to February 2013. We selected 20 farmer fields near the CARBAP Research Station (4° 34' 11.33'' N; 9° 38' 48.96'' E; 79 m a.s.l.) with similar environmental conditions for all of the fields, which have a young brown soil derived from a volcanic platform (Delvaux et al., 1989). The climate is humid tropical with a monthly mean temperature ranging from 25.0 to 27.4°C and a mean annual rainfall of 2610 mm. All fields contained plantain crops (*Musa AAB* genome) and a diverse array of other annual and perennial crops. Pesticides and fertilizers are rarely applied in these extensively managed systems.

In each field, we conducted the samplings of ants and cultivated plants in one 12 X 12 m plot which was subdivided into 25 square sites of 2.4 X 2.4 m. We performed samplings during two periods: the rainy season (mid-March 2012 to mid-November 2012), the dry-season (mid-November 2012 to February 2013).

VEGETATION STRUCTURE AND DIVERSITY

For each site of each field, we identified all crop plants, measured their respective density (number of plants of each species by square meter) and recorded their coordinates with a measuring tape

(using site corners as the reference to minimize error). We classified the plant species into four categories: low stratum, medium stratum, high stratum and musa group. For each category, we calculated the density of plants per square-meter. Plant diversity of each site is assessed by the Shannon Index (Shannon, 1948), which was calculated with the 'diversity' function of the 'vegan' R package, (Dixon, 2003).

ANT COMMUNITY

In each site, we measured ant abundance by using attractive, canned tuna-honey baits (Josens et al., 2014), which were placed 0.5 m distant from each of the eight plantain plants in a unit, alternating from one side to the other with each adjacent plantain plant. The bait, which had a diameter of 4 cm, was placed in the center of a 30 X 30 cm white ceramic tile. Ants were collected with an aspirator after the 30 minutes period when the baits were deployed. The ants on white ceramic plates were digitally photographed, counted and identified according to the Bolton key (Bolton and Ficken, 1994) and the PIAkey (Sarnat, 2009). For each site, we attributed rank values for each ant species according to their respective abundances. We determined therefore the numerically dominant species for each site.

STATISTICAL ANALYSIS

We used linear generalized modeling framework for multinomial response variable to assess the effect of each stratum on the probability of being numerically dominant for each ant species. First, we tested for collinearity using the method of the variance inflation factors (VIF) (Zuur et al., 2009). Then, we used Akaike information criterion (AIC) and likelihood ratio tests (LRTs) to select the best model by removing non-significant parameters in a backwards-stepwise process using LRTs. The selection procedure was continued until a model was found in which all effects were significant (Zuur et al., 2009). Multinomial models were estimated using the 'VGAM' package (Yee, 2010).

We used the mixed modeling framework to assess plant diversity and interspecific interactions on the abundance of each studied ant species. Following Zuur et al. (2009), we first log-transformed the values of ant abundances to prevent large value effects on the correlation coefficients between variables. Then we tested for collinearity using the method of the VIF.

Once the set of explanatory variables (fixed effects) was determined, we tested the random effect structure. On a single season of samplings, diverse factors, such as humidity or temperature, may make the abundance of a species more similar between samplings. To consider the non-independence between samplings of a same season, we introduced the season as a random intercept effect. Similarly, on a single field, a multitude of local factors, including plot history, may make the abundance of a species more similar between sites of a same field than with sites of other fields, leading to pseudoreplication. To consider the non-independence between sites of a same plot, we introduced the plot number as a random intercept effect. On a single site, habitat structure, microhabitats and nesting sites may make the sampled abundances of a species measured on a same site non-independent. Therefore, we nested the random site effect within the plot effect. Following Zuur et al.(Zuur et al., 2009), we tested random effect structures by comparing nested generalized linear mixed model (GLMM) with a Poisson error comprising all fixed effects. We used AIC and LRTs to select the best random effect structure of the model for each ant species (Bolker et al., 2009).

After determining the best random structure for each species GLMM, we selected the best model by removing non-significant fixed-effect parameters in a backwards-stepwise process using LRTs. The selection procedure was continued until a model was found in which all effects were significant (Zuur et al., 2009). All GLMMs were estimated using the 'glmer' function in the 'lme4' package (Bates et al., 2012), in which the maximum likelihood of parameters is approximated by the Laplace method (Bolker et al., 2009).

All statistical analyses were performed with R 2.15.0 (R Development Core Team, 2014) and with an alpha level of 0.05.

Results

ANT COMMUNITY

Overall, we measured 20 910 ants belonging to 14 species. We retained six taxa of ants by deleting less abundant species and combining abundances of species of same generous: *Pheidole, Monomorium and Camponotus* respectively in *Pheidole* spp., *Monomorium* spp. and *Camponotus* spp*. Pheidole* spp. were the most abundant taxa with 9200 individuals followed by *Camponotus spp.* with 3044 individuals, *Tetramorium* sp. with 3027, *Monomorium* spp. with 3027, *Paratrechina longicornis with 1562* individuals and *Axinidris* sp. with 895 individuals.

Frequencies of dominance are similar regarding to the season of samplings (**Figure 1**).The most frequently dominant species is *Pheidole* spp. followed by *Camponotus* spp., *P. longicornis* and *Monomorium* spp. (**Figure 2**), and the less frequently dominant species are *Tetramorium sp.* and *Axinidris sp.* (**Figure 1**).

EFFECT OF VEGETATION STRATA ON DOMINANCE OF ANTS

We collected 31 plant species which were grouped in four vegetation strata according to theirs height (**Table 1**). We found significant differences between the probabilities of dominance of each species (**Table 2**). We found that the medium and high strata significantly affected the probability of dominance of ant species (**Table 2**). Dominance of species *Pheidole* spp., *Monomorium* spp. and *Tetramorium sp.* are negatively correlated with the medium and high strata, whereas *P. longicornis, Camponotus* spp, and *Axinidris sp.* are positively correlated with the medium and high strata (**Figure 3**).

EFFECT OF PLANT DIVERSITY AND INTERSPECIFIC INTERACTIONS ON ANT ABUNDANCE

The abundance of *Pheidole* spp. and *Tetramorium* sp. was positively related to the plant diversity (resp. LRT: $P < 0.001$, $\chi^2 = 41.27$, df = 1; LRT: $P < 0.001$, $\chi^2 = 23.07$, df = 1). The abundance of of *P. longicornis*, *Axinidiris sp. Monomorium* spp. was negatively related to the plant diversity (resp. LRT: $P < 0.001$, $\chi^2 = 19.49$, df = 1; LRT: $P = 0.021$, $\chi^2 = 5.32$, df = 1; LRT: $P < 0.001$, $\chi^2 = 16.36$, df = 1). The abundance of *Camponotus* spp was not affected by the plant diversity (LRT: $P = 0.75$, $\chi^2 = 0.10$, df = 1) (**Figure 4**). For clarity of the manuscript, statistical results on the effect of interspecific interactions on each ant species are recorded in the supplementary material **Table S1** and summarized in **Figure 5**. Among the 15 pairwise interspeicific interactions, we found that 7 are symmetrically antagonistic (-/-), 4 are neutral/antagonistic (NS/-), 1 is symmetrically neutral (NS/NS), 2 are neutral/positive and 1 is symmetrically positive (+/+). We found that the season random effect improved significantly the GLMM on abundance for *Pheidole* spp., *Tetramorium* sp., *Monomorium* spp. but not for *P. longicornis* and *Camponotus* spp (**Table S1-S6**). We found that the field random effect improved significantly the GLMM on abundance for all ant species (**Table S1-S6**). We found that the site random effect improved significantly the GLMM on abundance for *Pheidole* spp., *P. longicornis*, *Monomorium* spp. and *Camponotus* spp spp. (**Table S1-S6**).

DISCUSSION

EFFECT OF VEGETATION STRATA ON DOMINANCE OF ANTS

We aimed to assess the effect of the different vegetation strata on the numerical dominance of each species. First we found that basic dominance probability is higher for *Pheidole* spp. than for the other ant taxa. This is consistent with general literature on ants where *Pheidole* genus is considered as a generalized Myrmycinae, sub-dominant to dominant Dolicherinae (van Ingen et al., 2008). As we observed no ants of Dolichoderinae family, it is not surprising that *Pheidole* taxa dominate ecologically the plantain-based field. Abera-Kalibata et al. (2008) found that *Pheidole* spp. were the most abundant ant taxa in banana fields in Uganda. We observed similar frequencies of dominance for the crazy ant *P. longicornis*, *Camponotus* spp. and *Monomorium* spp. These results agree also the ant literature, where *Monomorium* genus is considered as a generalized Myrmycinae sub-dominant to dominant Dolicherinae, *Camponotus* spp., as a ubiquitous sub-dominant that may numerically dominate arboreal vegetation (Davidson, 1997; Tadu et al., 2014). The tramp crazy ant *P. longicornis* is known to be an exploitative competitor unlike the other dominant species, which are interference competitors and uses a foraging strategy short-range recruitment (Kenne et al., 2005). The dominance of *P. longicornis* at baits is principally linked to its speed (Kenne et al., 2005). We found that *Tetramorium sp*. and *Axinidris* sp. are less frequently dominant species.

We found that the general trend of dominance can be counter-balanced by the medium (shrubs) and high (trees) strata. We showed that the probability of being dominant for ground-dwelling ants like *Pheidole* spp., *Monomorium* spp. and *Tetramorium* sp. logically decrease as the density of shrubs and trees increases, whilst the probability of being dominant for the arboreal species *Camponotus* spp. and the tramp species *P. longicornis* increases with shrubs density. Tree density has also a positive effect on these species, but when tree densities are higher, the dominance probability of the strictly arboreal ant *Axinidris* sp. rises. We found no effect of the low strata on dominance of ants. Stevens et al. (2002) found no effect of ground cover on dominance of the Dolichoderinae ant *Iridomyrmex* in citrus groves. Put together, these results suggest that low stratum do not modify directly habitats for functional groups to which the 6 studied species belong (Andersen, 1995). However, the low stratum may have influenced the cryptic functional group of ants (e.g. hypogaeic and litter-dwelling ants), such as demonstrated by Bestelmeyer and Wiens (1996), but this is not in the scope of our study.

Following Ribas et al. (2003), shrub and tree densities may influenced ant communities through three processes : (i) resources increase with shrub and tree densities, allowing more diversity in ant species; (ii) the habitat conditions are altered by shrub and tree densities, therefore conditioning the dominance hierarchies in ant communities; (iii) the variation in shrub and tree densities leads to species-area patterns. We do not test here the effect of vegetation diversity and structure on the species richness of ant communities. Our results on dominance hierarchies are in agreement with the second and third processes. Indeed, the effects of strata densities are coherent with the preferential ecological niche of the 6 studied ant species. Ground-dwelling species are here negatively related to the density of arboreal habitats (e.g. shrubs and trees). This agrees Lassau & Hochuli (2004) results which demonstrated that species that only nest on ground are negatively related to density of tree cover. *Camponotus* spp., which may forage both on ground and in arboreal strata but generally nest in dead or living stems, are positively relate to the density of arboreal habitats, except in the extreme densities of trees which coincides the dominance of *Axinidris* sp. This species nest strictly in trees and are primarily arboreal foragers but may occasionally forage in ground litter (Snelling et al., 2007). We observed *Axinidris* sp. individuals at baits only in the dry season, which is consistent with previous suggestions that assume arboreal ant species forage at ground-level during the dry season, when resources in trees are relatively low (Delabie et al., 2000). *Paratrechina longicornis*, known as the crazy ant, is a native species of West Africa and prefer moist habitat for reproduction (Kenne et al., 2005). The nests of this tramp species are often small and ephemeral and occur in a wide range of habitat (e.g. plant cavities, live or dead plants, leaf litters). An increase in shrub and tree densities may affect local hygrometry and increase the density of available nesting sites, favoring the establishment of *P. longicornis* colonies. Thus an increase in the shrubs and trees densities may for indeed, it is likely that sites displaying a more complex vegetation structure produces more litter and shade and, consequently, affect the entire invertebrate communities by providing more resources and habitats (Vasconcelos and Laurance, 2005). However, *P. longicornis* is known to be a feeble competitor against most frequent ground-dwelling ant species (including *Camponotus* spp.*)* in its native range (Kenne et al., 2005). We may hypothesize here that as tree densities increase in an area and, thus, availability of foraging and nesting sites increase, better competitors such as *Camponotus* spp. and *Axinidris* sp. dominate the area (Vasconcelos et al., 2008).

Therefore, manipulating the densities of cultivated shrubs and trees may be a way to maintaining coexistence of ant species through the arrangement of different habitat patches. For management purposes, the effects of plant diversity and interspecific interactions on ant abundances should also be considered (Parr, 2008; Ribas and Schoereder, 2007).

EFFECT OF PLANT DIVERSITY AND INTERSPECIFIC INTERACTIONS ON ANT ABUNDANCE

We found a positive relationship between the abundance at baits of *Pheidole* spp. and *Tetramorium* sp. with the plant diversity, whilst *P. longicornis*, *Monomorium* spp. and *Axinidris* sp. respond negatively to increase in plant diversity. We can propose three different mechanisms to explain such responses: (i) disturbed/undisturbed habitat preference; (ii) diet and behavioral consequences; (iii) abundant resources favors dominant species. *P. longicornis*, which originated from West Africa (Kenne et al., 2005), is known as an invasive species in many tropical and sub-tropical areas and is generally associated with disturbed environments. The same holds for some tramp species of the *Monomorium* genus which is, according to Hanson & Gauld (1995) behave similarly to *Solenopsis* ant and are often associated to disturbed habitats. Therefore, *P. longicornis* and *Monomorium* spp. may be favored in low diversified habitats which characteristics corresponds to highly disturbed habitats such as monocultural agrosystems. Secondly, plant diversity is likely to provide more temporally constant carbohydrate sources to ants, through extra-floral nectarines or hemipteran/homopteran honeydew. It has been recently shown in *Formica podzolica* that excessively carbohydrate-fed ants drastically lowered their foraging activities (Petry et al., 2012). Therefore, negative impact of plant diversity on abundances of *P. longicornis*, *Monomorium* spp. and *Axinidris* sp. may be explained by an increase in exploitation of honeydew and extra-floral nectaries. This may be particularly true for *P. longicornis* because Formicinae possess a particular postventricular structure that is typical of ants that forage extensively for large quantities of exudates (Davidson, 1997). Moreover, the ecological dominance of *P. longicornis* has recorded to coincide with high densities of homopterans (Wetterer et al., 1999). As plant diversity increase, it is likely that resources abundance and quality (e.g. prey, honeydew or extra-floral nectaries) increase. In this context, dominant species is assumed to increase in abundance (Davidson, 1997; Palmer, 2003). Here, *Pheidole* spp. is ecologically dominant and the observed positive correlation with plant diversity is congruent with theoretical predictions (Davidson, 1997; Palmer, 2003). Elsewhere, surplus of carbohydrate can increase the aggressiveness of foragers, predation rates and foraging activity (Davidson, 1997; Grover et al., 2007; Kay et al., 2010). The positive relationship between abundance of *Pheidole* spp. and *Tetramorium* sp. at baits may results from one or several these effects due to carbohydrate excess, leading the species to shift their foraging activity to the limited resource, that is protein. However, Petry et al. (2012) recently found, in the ant *Formica podzolica*, that carbohydrate excess induces a drastic decrease of ant foraging activity. We found no relationship between *Camponotus* genus and plant diversity. One explanation may be that most of *Camponotus* species forage both arboreally and on the ground, but have specialized nesting habits, founding colonies generally in living or dead trunks. Davidson

(Davidson, 1997) argued that such ant species place their nest close to preferred resource plants. Consequently, plant diversity would not modify their nesting or foraging habits.

Most of coefficients of interspecific interactions are symmetrically antagonistic, suggesting that interference competition prevail in these ant communities. Interestingly, among these symmetrically antagonistic interactions, we found all the combination of pairwise interactions between the four most frequently dominant taxa (e.g. *Pheidole* spp., *P. longicornis*, *Monomorium* spp. and *Camponotus* spp.). This supports the findings of Parr (2008) who showed that, in South African savanna, dominant species at baits can control species composition at the assemblage level, However, "momentary" regulation of ant communities (i.e. at baits) do seem to always reflect the species composition at the assemblage level and may depend on the type of ecosystem (Baccaro et al., 2012). Elsewhere, *Camponotus* spp. and *P. longicornis* display only negative effects on abundance of others species, leading to the conclusion that these species are exclusively interference competitors. This contradicts the fact that *P. longicornis* is an exploitative competitor (Kenne et al., 2005).

Monomorium spp., *Tetramorium* sp., *Axinidris* sp. and *Pheidole* spp. display different signs of interactions, and one other interesting finding is the symmetrically positive interactions between the ground-dwelling taxa *Pheidole* spp. and the arboreal species *Axinidris* sp. These results suggest that ants may modulate their behavior of resource domination (e.g. aggressiveness) according to the co-occurent species they face. Such unclear pattern of species interaction has also been recently demonstrated in ant communities of temperate agrosystem (Chong et al., 2011).

MANAGING THE VEGETATION STRUCTURE TO FAVOUR ECOSYSTEM SERVICES

We have here demonstrated the importance of vegetation structure on the community assemblage of ants in diversified plantain-based agrosystems. By manipulating the tree and shrub density, famers may improve different ecosystem services. First, diversifying agrosystems will lead to coexistence of different ant species in the same field. In a meta-analysis study, Rosumek et al. (2009) have shown that experimental ant removal increase herbivore abundances and herbivory rates, despite an increase in predator abundances, and that plant reproduction is negatively impacted. They also show that ant removal is more impacting in tropical regions than in temperate ones, resulting in a decrease of 59% of the plant fitness. Therefore, ants are largely involved in plant defense and their presence may be economically substantial in cultivated systems. Elsewhere, ants have increasingly been recognized as important predators in agricultural systems of tropics and subtropics (Perfecto and

Castineiras, 1998; Way and Khoo, 1992). Ants have complex and often strong effects on lower trophic levels (Philpott et al., 2008) and may be useful in pest management (Perfecto, 1991). For instance, the banana weevil, *Cosmopolites sordidus* is the most important pest in plantain production areas (Gold et al., 2001). Recently, Mollot et al. (2014) have shown, through metabarcoding analysis, that the carpenter ant *Camponotus sexguttatus* and the fire ant *Solenopisis geminata* prey on *C. sordidus*, which are respectively arboreal and ground-dwelling ants. We have here shown that *Camponotus* spp. are favored by presence of shrubs and trees but suffer interference competition from other dominant species. We evidenced also a positive link between *Pheidole* spp. and *Tetramorium* sp. and plant diversity. Yet, Abera-Kalibata et al. (2007) have suggested *Pheidole* as a potential natural enemy of *C. sordidus* and *Pheidole megacephala* and *Tetramorium guinensee* are used as biological control agents of *C. sordidus* in Cuba (Castineiras and Ponce, 1991; Perfecto and Castineiras, 1998). Therefore, by introducing heterogeneity in the density vegetation strata or diversity, it should be possible to increase dominance of desired species for *C. sordidus* regulation and modify the issue of interspecific competition according to the per capita rate of pairwise interactions we have found. Moreover, according to the insurance hypothesis (Yachi and Loreau, 1999), diversified agrosystems are more likely to maintain ecosystem services when alteration of the agrosystems (e.g. harvest) occurs. Moreover, such resilience of the agrosystems may be beneficial (Baumgartner and Strunz, 2014). By a theoretical and conceptual approach, these authors demonstrated the insurance value of resilience is negative for low levels of resilience and positive for high levels of resilience. In other words, the ecosystem resilience acts as insurance by decreasing the riskiness of income from the ecosystem services.

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Table 1. Cultivated plant species in each stratum

Stratum	Cultivated plant species
Low	groundnut, cocoyam1, cocyam2, yam , hot pepper, garden egg, *Corchorus* spp., pineapple, *Amaranthus*, tomato, gombo, cowpea, sweet potato, maize
Medium	Papaya, cassava, *Vernonia spp.*, *Gnetum afrincanum, Triumfetta spp.*
High	palm, coffee, cocoa, cola, safou, avocado, guava, mango, lime, orange
Musa	banana, plantain

Table 2. Likelihood ratio tests for the Strata multinomial model.

Variables	Δ d.f.	Chi²	p-value
Intercepts	5	333.29	< 0.0001
Shrubs	5	33.14	< 0.0001
Trees	5	18.85	0.002
Musa	5	9.82	0.08
Low stratum	5	6.11	0.30

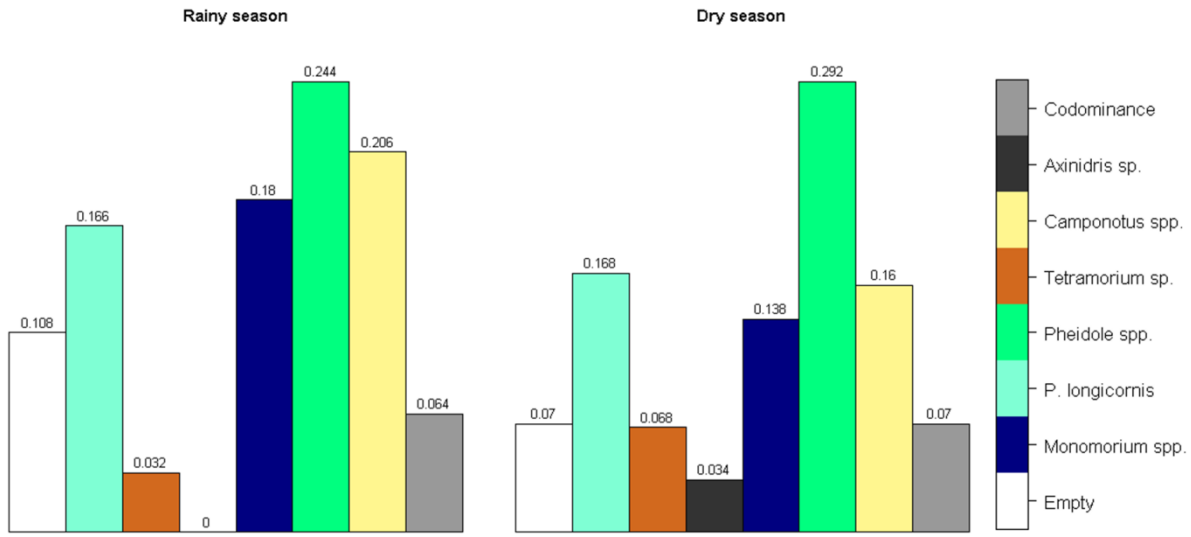

Figure 1. Frequencies of dominance for each ant species in the rainy and dry seasons.

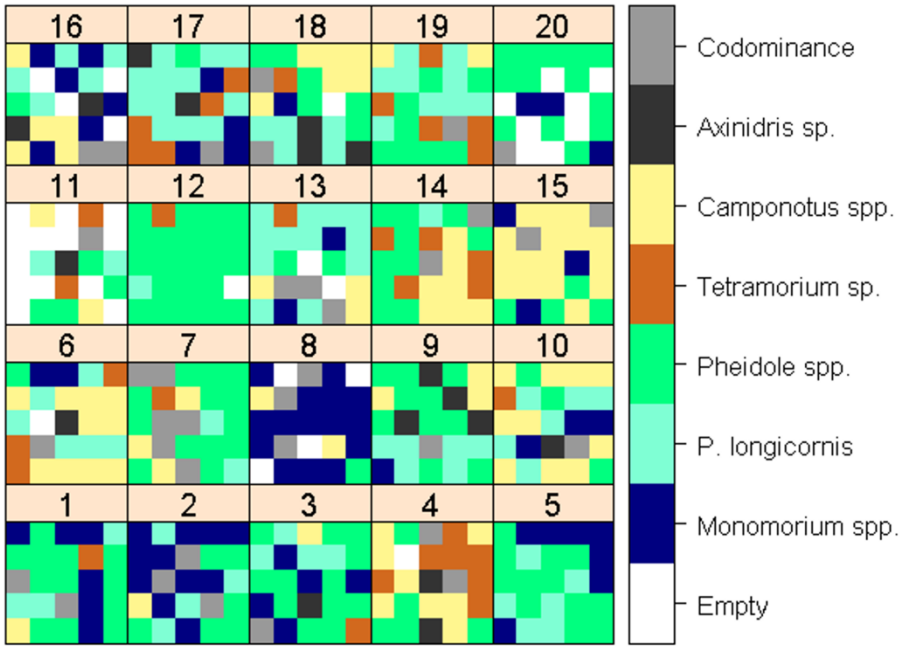

Figure 2. Site dominance for each ant species (dry season). Numbers correspond to field identification

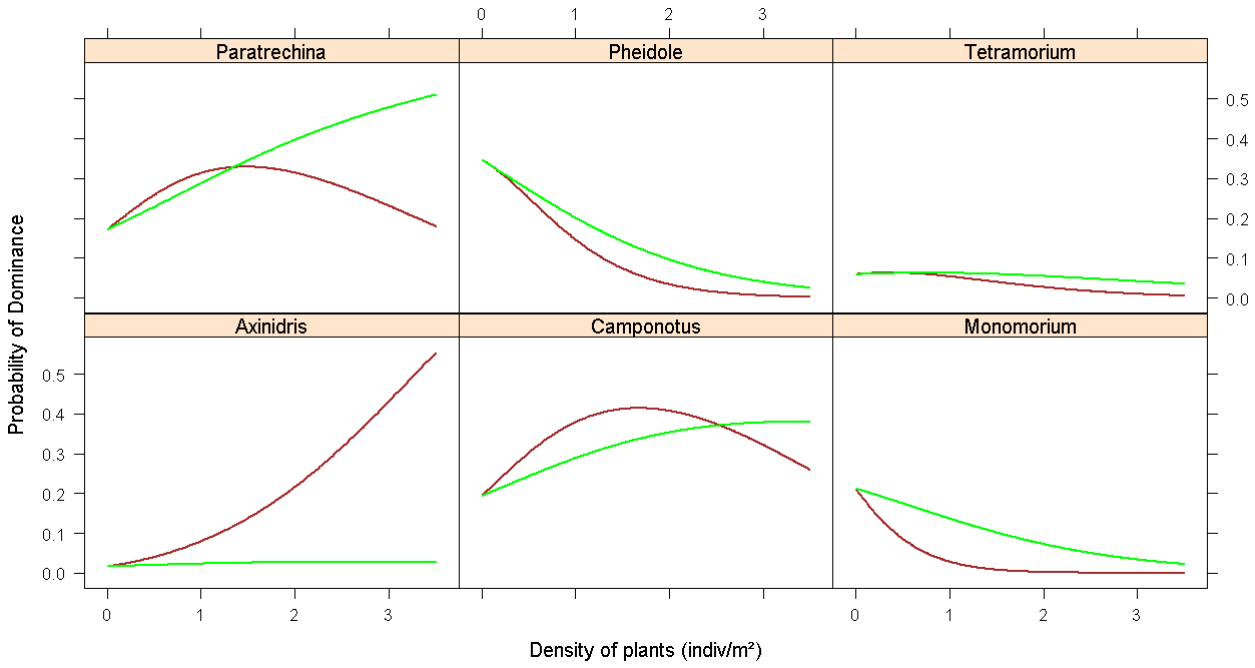

Figure 3. Prediction of the frequencies of dominance for each ant species according to the density of trees and shrubs. Brown curves : Response to tree density; Green curves : Response to shrub density.

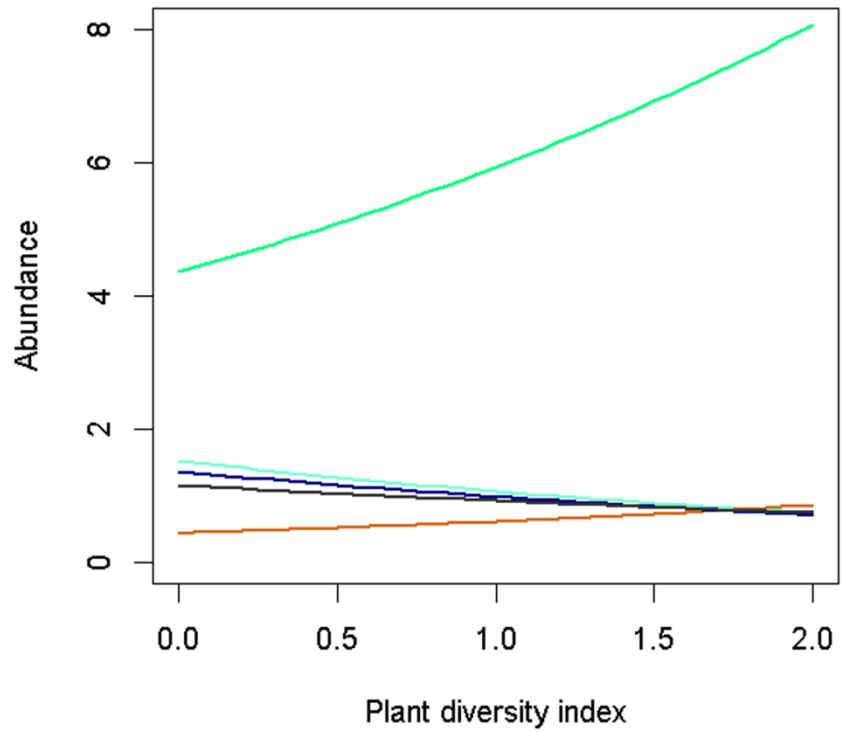

Figure 4. Predictions of the GLMM on the abundance of each ant species according to variation in plant diversity (Shannon Index). Green curve: *Pheidole* spp.; Orange curve; *Tetramorium* sp.; Cyan curve: *P. longicornis*; Blue curve: *Monomorium* spp.; Dark gray curve: *Axinidris* sp.

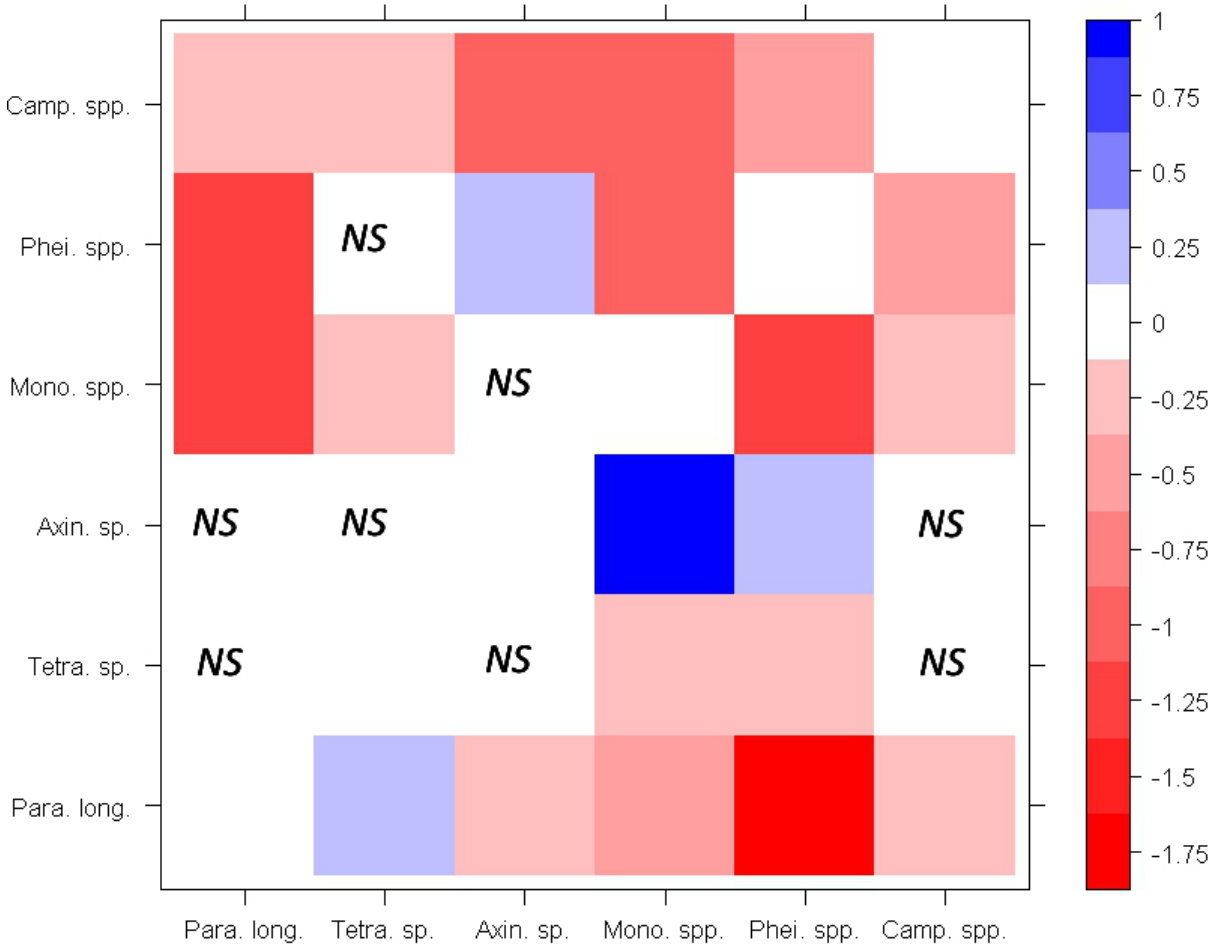

Figure 5. Estimates of interspecific interactions with species in y-axis affecting abundance of species in x-axis.

SUPPLEMENTARY MATERIAL

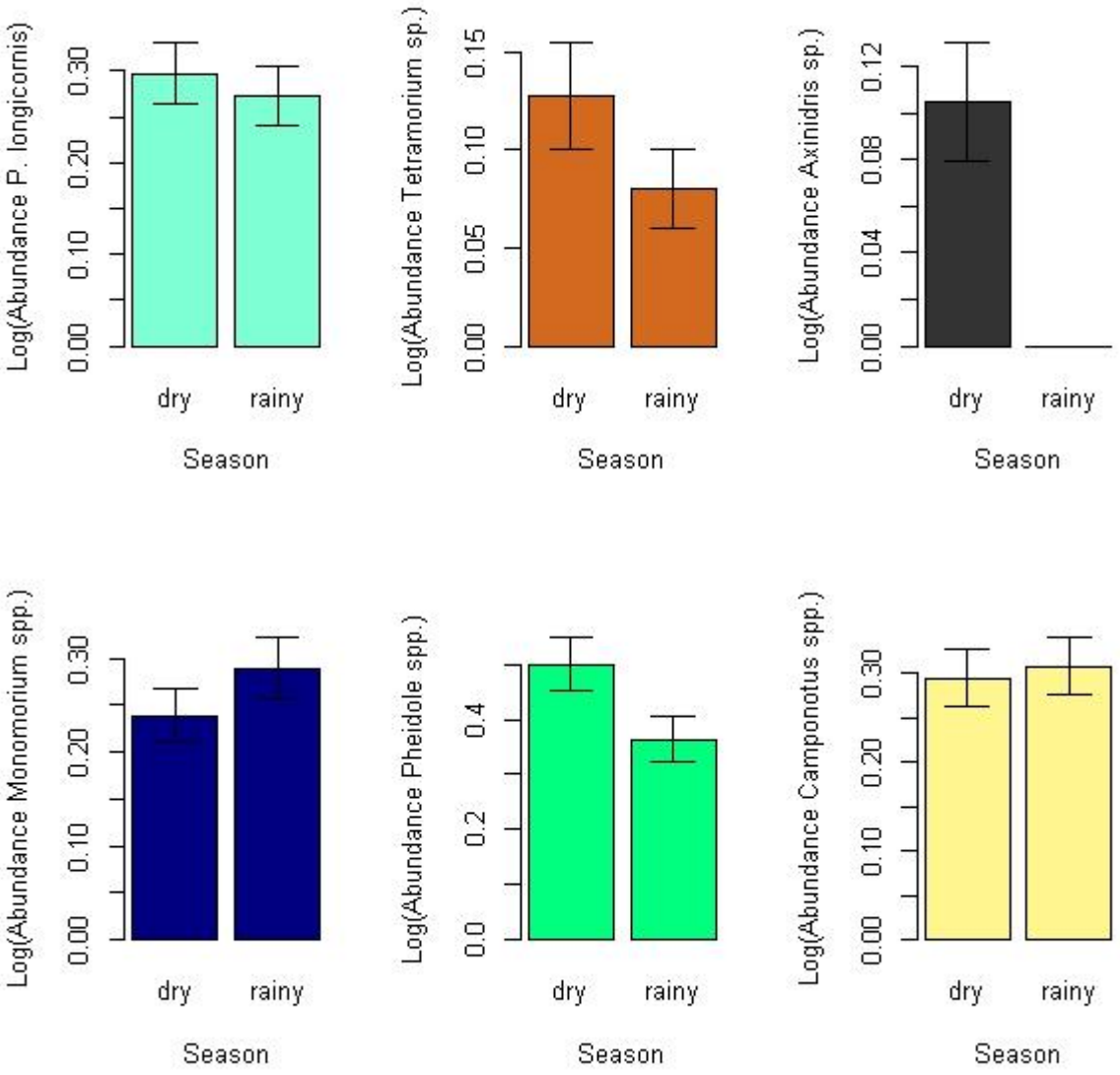

Figure S1. Log of the mean of abundance of each ant species in the rainy and dry seasons.

Table S1. Results of backwards-stepwise selection of GLMMs to assess plant diversity and interspecific interactions for each ant species.

	Plant diversity	*P. longicornis*	*Tetramorium*	*Axinidris*	*Monomorium*	*Pheidole*	*Camponotus*
P. longicornis							
Chi2	19.49	-	0.17	2.64	142.07	339.17	63.37
p-value	< 0.001		0.68	0.10	< 0.001	< 0.001	< 0.001
Tetramorium							
Chi2	23.07	9.28	-	1.42	30.07	1.12	24.00
p-value	< 0.001	0.002		0.23	< 0.001	0.29	< 0.001
Axinidris							
Chi2	5.32	10.91	3.45	-	1.61	16.05	94.92
p-value	0.02	< 0.001	0.06		0.20	< 0.001	< 0.001
Monomorium							
Chi2	16.36	74.90	20.88	47.19	-	279.78	69.96
p-value	< 0.001	< 0.001	< 0.001	< 0.001		< 0.001	< 0.001
Pheidole							
Chi2	41.27	1141.94	15.66	28.43	377.33	-	386.37
p-value	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001		< 0.001
Camponotus							
Chi2	0.10	19.60	0.08	0.97	37.00	292.01	-
p-value	0.75	< 0.001	0.77	0.32	< 0.001	< 0.001	

Chapitre 3. Quel est l'effet des cultures fréquemment associées aux plantains sur la structure de la communauté des fourmis et le control de *C. sordidus* ?

Ce chapitre vise à comprendre comment les cultures associées au plantain peuvent modifier la régulation biologique de *C. sordidus*. Ce chapitre repose sur un article accepté à Biological Control et est intitulé <**Ant abundance and *Cosmopolites sordidus* damage in plantain fields as affected by intercropping>.**

Le premier objectif était de voir comment un petit nombre de plantes associées au plantain modifient les communautés des fourmis et les dégâts de *C. sordidus*. Nous avons réalisé un essai sur la station d'expérimentation du Centre Africain de Recherches sur Bananiers et Plantains (CARBAP) à Njombé. Il s'agissait d'une parcelle de 1ha de plantain en 3^{e} cycle comportant 833 plants de plantains. Nous avons subdivisé la parcelle en quatre blocs comportant chacun huit traitements de cultures associées couramment cultivées au Cameroun en association avec le plantain. Les cultures associées étaient du macabo *Xanthosoma* sp., maïs (*Zea mays*), et pistache (*Lagenaria siceraria*). Ces trois cultures ont été cultivées en simple, double et triple association avec le plantain. Dans cette expérimentation, nous avons effectué un piégeage avec appâts pour capturer les taxas de fourmis afin déterminer les effets des cultures associées sur les communautés des fourmis. Nous avons aussi effectué un décorticage sur les bulbes des plants de plantain au début et à la fin de l'expérimentation pour évaluer les effets des cultures associées sur les dégâts des larves de *C. sordidus*. Le deuxième objectif était de déterminer la relation entre la communauté des fourmis et les dégâts des larves de *C. sordidus*.

Ant abundance and *Cosmopolites sordidus* damage in plantain fields as affected by intercropping

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Abstract

Intercropping is a practical way to increase plant diversity in agroecosystems and provide alternative food and habitat to arthropods, including generalist predators. In tropical agriculture, ants are important predators and have complex and often strong effects on pests. With the goal of optimizing control of the banana weevil, *Cosmopolites sordidus*, we studied maize (*Zea mays*), cocoyam (*Xanthosoma sagittifolium*), and bottle gourd (*Lagenaria siceraria*) as intercrops in a plantain field in Cameroon. We analysed the effects of intercropping on ant abundance (by taxon) and on the damage caused by *C. sordidus* larvae to plantain corms. We also analysed the relationship between ant abundance and *C. sordidus* damage. When added singly, the three intercropped plants significantly affected the abundance of each of the seven ant taxa but the sign of the effect depended on the intercropped plant species and on the ant taxon. Intercropping had clear effects on ant abundance, which was negatively correlated with *C. sordidus* damage for the Myrmicinae and positively correlated for the Formicinae and Ponerinae. Intercropping in plantain agroecosystems has the potential to alter ant community structure which contributes to *C. sordidus* control, but the effect of intercropped plant species remain unclear and further investigations are needed.

Keywords: Ant community, Biological control, Banana weevil, Cameroon, Feeding damage

1. Introduction

Plant diversity alters arthropod food webs by increasing the abundance of most trophic groups except for pests and invaders, which tend to decrease (Scherber et al., 2010). Increasing plant diversity in agroecosystems is a promising way to improve pest control (Brown, 2012). The diversification of agroecosystems increases the availability of habitats, alternative prey or hosts, and shelter for natural enemies (Landis et al., 2000). Intercropping is a practical way to improve plant diversity in agroecosystems, and several studies have shown that intercropping tends to favor natural enemies of pests and thus enhance biological control (Berndt et al., 2006; Hooks and Johnson, 2003; Song et al., 2010). However, mechanisms linking intercropping and pest control are complex because they include both direct effects (the provisioning of resources for alternative prey of generalist predators) and indirect effects (the modification of the entire community structure and the alteration of habitats). Intercropped plants, for example, may alter the entire arthropod community (Liang and Huang, 1994) and reduce pest populations by increasing the abundance of natural enemies (Khan et al., 1997; Risch, 1983). Interaction among the generalist predators may also be modified by increased plant diversity, e.g., increased plant diversity can decrease intraguild predation among generalist predators (Tixier et al., 2013) and thereby increase control of herbivores. Plant diversity may also increase the abundance of alternative prey, which usually enhances pest control but may reduce pest control if the pest is not the preferred prey (Koss and Snyder, 2005). Here, we investigate the effects of intercropping on the community of ants in plantain and on the damage of the banana weevil, *Cosmopolites sordidus* (Germar), to this crop.

Cosmopolites sordidus is a major pest in most banana and plantain production areas (Gold et al., 2001) including Cameroon (Okolle et al., 2009). Females lay their eggs on the plantain corm, and eclosing larvae bore galleries and feed in the corm (Koppenhöfer, 1993). If there is no management of the weevil population and infestation levels are high, the damage can be substantial and may even result in the death of banana plants (Rukazambuga et al., 1998). In commercial banana plantations, pheromone traps have been successfully used to reduce populations (Duyck et al., 2012). However due to the significant cost of pheromone trapping, this method is not suitable for small-scale plantain farmers in Centre Africa, and is not practical on large scale farms where control of *C. sordidus* is needed (Alpizar et al., 2012; Rhino et al., 2010).

Cosmopolites sordidus adults disperse by walking over the soil during the night (Vinatier et al., 2010) and may suffer significant mortality from generalist predators on the soil surface. For example, predation on *C. sordidus* by the ants *Odontomoachus brunneus* and *Pheidole fallax* was observed in the field in Martinique (Carval pers. Com). The egg stage is particularly vulnerable to generalist predators such as ants (Abera-Kalibata et al., 2007). Larval stages develop within the

banana plant (Abera-Kalibata et al., 1999) and are consequently inaccessible to many predators. However, Abera-Kalibata et al. (2006) observed predation of *C. sordidus* larvae by the ant *Myopopone castanea* Smith (Ponerinae). Generalist predators such as ants, earwigs, and ground beetles are all potential sources of mortality for *C. sordidus* (Abera-Kalibata et al., 2006; Mollot et al., 2014). Insect parasitoids of *C. sordidus* are scarce, and attempts at classical biological control of *C. sordidus* with them have been unsuccessful (Gold et al., 2001).

In Africa, plantains are grown in association with annual crops (root, tuber, and vegetable crops) and perennial crops (cocoa, coffee, palm, and others). Studies have shown that cover crops, used in banana plantations to reduce herbicide applications and erosion, increase primary productivity and diversify the basic resources available for higher arthropod trophic levels Duyck et al. (2011). In another study, addition of a cover crop also increased the abundance of the fire ant *Solenopsis geminata* (Myrmicinae) and, in turn, improved predation by this ant on eggs of *C. sordidus* (Mollot et al., 2012). Sweet potatoes and maize intercropping are known to increase *C. sordidus* natural enemies such as *Pheidole* sp., *Camponotus* sp., *Dorylus* sp., *Forficula* sp., and some tenebroinids (Uronu, 1992). However, other studies showed that the legume intercrops did not affect *C. sordidus* populations and damage (McIntyre et al., 2001). Intercropping may also alter *C. sordidus* damage indirectly because competition for nutrients with other plants may increase the susceptibility of plantains to *C. sordidus* (Gold et al., 2001; Rukazambuga et al., 2002). Here, we focus on annual crops as intercrops in plantain systems with the goal of understanding how their presence affects arthropod community structure and pest control in plantain agroecosystems with low chemical inputs.

Ants have been increasingly recognized as important predators in agricultural systems in the tropics and subtropics (Perfecto and Castineiras, 1998; Way and Khoo, 1992). Ants have complex and often strong effects on lower trophic levels (Philpott et al., 2008) and may be useful in pest management (Perfecto, 1991). The potential for ants to control insect herbivores, however, can depend on the structure of their community and on their feeding behavior. In banana agroecosystems in French Antilles, Mollot et al. (2012) documented the carpenter ant *Camponotus sexguttatus* feeding on *C. sordidus* and in Cuba, Roche and Abreu (1983) showed that *Tetramorium guineense* ants reduced *C. sordidus* populations in heavily infested banana plantations. In Uganda, Abera-Kalibata et al. (2008) found that *Pheidole* sp. and *Odontomachus troglodytes* Santschi reduced the density of *C. sordidus* eggs but not of larvae in banana suckers. Castenieras and Ponce (1991) reported that *Tetramorium guinensee* (Nylander) reduced *C. sordidus* populations in plantations with moderate to heavy *C. sordidus* infestations and that *Pheidole megacephala* (Fabricius) deterred *C. sordidus* oviposition on banana plants. Most studies have considered the effect of only one or few

ant species on *C. sordidus* and no study has yet addressed the impact of a whole ant community on *C. sordidus* control.

In the experiment described in this study, we planted three annual crops (tuber, cereal, and cucurbits) with plantain in single, double, and triple-species combinations. The general goal of the study was to determine whether and how intercropping may alter biological control of *C. sordidus* in plantain fields. The broad objectives were: i) to understand how these intercrops modify ant community structure in plantain fields and ii) to determine whether *C. sordidus* damage to plantain is correlated with the abundance of particular ant species. We also considered mechanisms of how intercropping might enhance biological control of *C. sordidus* in plantain fields.

2. Materials and methods

2.1. Study site and experimental design

Our study site was located at the CARBAP Research Station (4° 34' 11.33'' N; 9° 38' 48.96'' E; 79 m a.s.l.) in Njombe, Cameroon, Central Africa. The climate is humid tropical with a monthly mean temperature ranging from 25.0 to 27.4°C and a mean annual rainfall of 2610 mm. The young brown soil is derived from a volcanic platform (Delvaux et al., 1989). Seven intercropped treatments and one bare soil control treatment were tested in a field of plantain (AAB, *Musa acuminata x Musa balbisiana,* Batard variety) in its third cycle of production. Inside a 1ha plantain field (surrounded by other plantain fields), four replicates of 22m X 39m were defined with 6 m of bare soil separating adjacent plots. Each replicate was divided into eight experimental units (4 m X 22 m), one for each treatment, and each unit had a row of plantains running lengthwise down the middle so that there was a 2 m strip on each side of the row; bare soil was maintained or the intercrops were planted in these 2 m strips. Each experimental unit included eight plantain plants and was separated from other experimental units by a 1-m strip of bare soil. The intercropped treatments included three plants frequently associated with plantain in Cameroon: cocoyam, *Xanthosoma sagittifolium*, maize, *Zea mays*, and gourd, *Lagenaria siceraria*, representing a tuber-root, a cereal, and a cucurbit, respectively. The eight treatments included one control in which no other plant species was associated with the plantain, three single-species treatments with one companion plant, three double-species treatments with two companion plants, and one triple-species treatment. Plants in the double-species and triple-species treatments were homogeneously mixed around the plantains. Treatments were randomly assigned to experimental plots in each replicate. The intercropped plants were planted at the end of the third cropping cycle of plantain field and were maintained until the end of the fourth cropping cycle. To maintain continuous plant cover in the case of short-cycle maize

and gourd crops, replanting was conducted as needed. The plantains were uniformly fertilized (20% nitrogen, 10% phosphorous, and 10% potassium) at 500 kg per ha per year and all suckers were removed early in the cropping cycle, except for one selected for the next cropping cycle. Weeds were controlled manually in intercropped treatments and with herbicide (glyphosate) in the bare soil control treatment. The experiment began on March 1, 2013 and ended on February 28, 2014.

2.2. Sampling methods

2.2.1. Ant abundance

We determined the abundance of each ant species between June 1, 2013 and August 30, 2013 during the rainy season (from mid-March to mid-November) and again between December 1, 2013 and February 28, 2014 during the dry-season (from mid-November to February). In each experimental unit, we measured ant abundance by using attractive, canned tuna-honey baits, which were placed 0.5 m distant from each of the eight plantain plants in a unit, alternating from one side to the other of each adjacent plantain. The bait had a diameter of 4 cm and was placed in the centre of a 30 X 30 cm white ceramic tile All samples were obtained between 8:00 a.m. and 12:00 p.m. Ants were collected with an aspirator beginning 30 minutes after the baits were deployed. Ants on the ceramic tiles were counted, digitally photographed to later confirm the counts, and the ants identified using the Bolton key (Bolton and Ficken, 1994) and the PIAkey (Sarnat, 2009).

2.2.2. Ant abundance and corm damage by *C. sordidus*

At the end of the experiment, we measured the damage caused by *C. sordidus* larvae to plantain corms in experimental units. Damage assessment was done after shelling 2 cm of the corm surface from 10 cm above to 10 cm below ground over entire circumference of the corm. A 0 to 100 scoring system (Vilardebo, (1973) was used to score damage where 0 = no damage;,5 = 1 or 2 galleries per corm, and 10, 30, 40, 60, and 100 equaled 10, 25, 50, 75, and 100% of the corm circumference damaged, respectively. We also tested whether the Vilardebo method is reasonably correlated with real *C. sordidus* damage. On a total of 32 plants (one per experimental unit), we conducted a complete corm transverse section on which we measured the percentage of damage including deep galleries. There was a reasonable ($R^2 = 0.4864$) and significant ($P < 0.0001$) correlation between the percentage of damage on the corm section and Vilardebo damage index (**Fig. S1**).

2.3. Data analysis

We used generalised linear mixed models (GLMMs) with a Poisson error (O'Hara and Kotze, 2010) to analyse the effect of the intercropped plants and their interactions (double and triple) on each ant taxon and on the corm damage index. In all analyses, the statistical unit was the plantain plant on which measurements were taken. When local ant communities are dominated by one or a few species, ground baits can give misleading estimates of biodiversity (Folgarait, 1998). To consider the potential influence of locally abundant species on the effect of the intercropped plant(s) and the abundance of ant taxa, we included the sum of the local abundances of other ant species as a random factor. We verified the normality of the distribution of models' residuals (**Table S1 and S2**). We verified that data followed a Poisson distribution and log-transformed the ant abundance data to homogenize variation between species with small and large colonies. We considered the plantain plant as a random, individual effect. The HSD test (de Mendiburu and de Mendiburu, 2014) was used to group treatments according to level of *C. sordidus* damage .

We examined the need to include random effects using likelihood ratio tests (LRTs) (Bolker et al., 2009). Then, we removed non-significant fixed-effect parameters in a backward, stepwise process using LRTs, removing non-significant interactions first, and then non-significant variables. This procedure was continued until a model was found in which all effects were significant (Zuur et al., 2009). All GLMMs were estimated using the 'glmer' function in the 'lme4' package (Bates et al., 2012), in which the maximum likelihood of parameters is approximated by the Laplace method (Bolker et al., 2009). Statistical analyses were performed with R 2.15.0 (R Development Core Team, 2014) and with an alpha level of 0.05.

3. Results

3.1. Ant abundance

Ant abundance was similar in both the rainy and the dry season (**Table S1**) so the data was pooled for further analysis. A total of 12,197 ants belonging to 14 species were observed. We reduced the 14 taxa to seven by combining species by genera into three groups: *Pheidole* spp., *Monomorium* spp., and *Camponotus* spp. *Pheidole* spp. was the most abundant taxon with 4,681 individuals, followed by *Paratrechina longicornis* with 2,577 individuals, *Tetramorium* sp. with 2,182 individuals, *Monomorium* spp. with 1,555 individuals, *Camponotus* spp. with 755 individuals, *Axinidris* sp. with 390 individuals, and *Odontomachus mayi* with 57 individuals. The ants were distributed among

treatments as follows: 2,767 in cocoyam, 2,064 ants in cocoyam-gourd, 1,989 ants in gourd, 1,901 ants in controls, 1,170 ants in cocoyam-maize, 821 ants in maize, 803 ants in cocoyam-maize-gourd and 682 ants in maize-gourd treatment. Intercropping of plantain with one plant (maize, cocoyam, or gourd) significantly affected all seven ant taxa in all but one of the 21 cases (cocoyam did not affect *P. longicornis*) (**Fig. 1**). The effect of intercropping with more than one plant was significant for 12 of 21 cases with two added plants and for 2 of 7 cases with three added plants (**Fig. 1** and **Table S3**). Intercropping with gourd reduced the abundance of all seven ant taxa except *Pheidole* spp., whereas intercropping with maize and cocoyam reduced or increased ant abundance depending on the ant taxon.

3.2. Ant abundance and corm damage by *C. sordidus*

There was a significant effect of intercropping treatment on *C. sordidus* damage ($P < 0.0001$) but no treatment was significantly less damaged than controls (**Table 2**). Overall, the mean damage score was 34.69 ± 2.17 and ranged from 0 to 100. Although the damage demonstrated no clear relationship with intercropping, it was significantly related to the abundance of each ant taxon (**Fig. 2**). Damage was negatively related to the abundance of *Axinidris* sp. (LRT: $P < 0.001$, $\chi^2 = 11.15$, df= 1), *Monomorium* spp. (LRT: $P < 0.001$, $\chi^2 = 13.95$, df = 1), *Pheidole* spp. (LRT: $P < 0.001$, $\chi^2 = 16.06$, df = 1), and *Tetramorium* sp. (LRT: $P < 0.01$, $\chi^2 = 7.83$, df = 1). In contrast, damage was positively related to the abundance of *Camponotus* spp. (LRT: $P < 0.001$, $\chi^2 = 27.67$, df = 1), *Odontomachus mayi* (LRT: $P < 0.001$, $\chi^2 = 19.42$, df = 1), and *Paratrechina longicornis* (LRT: $P < 0.001$, $\chi^2 = 30.83$, df = 1).

4. Discussion

4.1. Ant abundance

Our results show that intercropping plantain with maize, cocoyam, or gourd significantly affected ant abundance but that the sign of this effect (positive or negative) depended on the intercropped plant(s) and on the ant taxon. The similarity of the ant community structure between seasons (**Table S1**) suggests that climatic conditions were not a main factor structuring the ant community. Maize had a positive effect on the abundance of *Camponotus* spp., *Monomorium* spp., and *Odontomachus mayi*, suggesting that these ant taxa may directly consume maize, may consume prey feeding on maize, or may otherwise benefit from maize habitat. The hypothesis that maize provides alternative

prey for predators is supported by other studies. For example, Perfecto and Sediles (1992) showed that pupae of armyworm, *Spodoptera frugiperda*, and corn leafhopper, *Dalbulus maidis*, were more abundant in a maize agroecosystem when ant abundance had been reduced with insecticides, suggesting that these pests were ant prey. Dejean et al. (2000) documented competitive interference between the ants *Camponotus acvapimensis*, *Crematogaster* sp., *Pheidole megacephala*, and *Myrmicaria opaciventris*; because of this interference, the maize pest *Peregrinus maidis* was more abundant when attended by multiple species of ants rather than by a single species. Another study showed that maize attracted predatory ants which, in turn, reduced maize damage by termites (Sekamatte et al., 2003).

In contrast to its positive effects on *Camponotus* spp., *Monomorium* spp., and *Odontomachus mayi*, maize had strong negative effects on *Paratrechina longicornis*, *Pheidole* spp., *Tetramorium* sp., and *Axinidris* sp. These could be partly due to the intensive cultural practices required by maize. Because of its short, 3 month cycle in our plots it was frequently reseeded, which may have caused disturbance of ants. The intensive farming practices of maize (weed control, irrigation, fertilization, tillage, and reseeding) may also have disturbed these particular ant taxa. Several studies have shown that agricultural practices such as heavy grazing, irrigation, drainage, fertilization, tillage, and planting can all reduce ant biodiversity and abundance (Díaz, 1991; Folgarait, 1998; Perfecto and Snelling, 1995).

Cocoyam had a positive effect on the abundance of *Axinidris* sp., *Camponotus* spp., *Odontomachus mayi*, and *Pheidole* spp., but a negative effect on the abundance of *Monomorium* spp. and *Tetramorium* sp. Overall, ants were more abundant in plots intercropped with cocoyam than the other two crops. Tubers and ants are known to be involved in mutualisms (Giusto et al., 2001) where ants defend the plant from insect defoliators and the plant provides nesting sites for the ants (Heil and McKey, 2003; Rosumek et al., 2009). Such a mutualism between ants and cocoyam is likely to play an important role in shaping the ant community.

Gourd plants reduced the abundance of all ant taxa except *Pheidole* spp. Gourd is a tendril-bearing, annual plant with unisexual flowers that are visited by many insects, including ants (Kost and Heil, 2005). Agarwal and Rastogi (2010) showed that *Pheidole* sp. was one of the most abundant ants visiting leaves, bracts, bracteoles, calyces, and flowers of gourd, protecting them against herbivores. Several studies showed a negative interaction between *Pheidole* spp and other predators involved in pest control (González-Hernández et al., 1999; Reimer et al., 1993). *Pheidole* spp. display often an aggressive behaviour towards subordinate species, which combined with its numerical dominance on various plant parts (Agarwal and Rastogi 2010), probably contributed to its rapid colonization of baits.

Ant abundance was more affected by intercropping with gourd- cocoyam than with gourd-maize or cocoyam-maize. The gourd-cocoyam treatment had a positive effect on *Camponotus* spp., *Monomorium* spp., and *Tetramorium* sp. and a negative effect on *Odontomachus mayi* and *Pheidole* spp. We suspect that ant abundance was more affected by gourd and cocoyam than by maize because these plants have longer crop cycles than maize. Surprisingly, intercropping with all three crops significantly affected the abundance of only two of the seven ant taxa, *Tetramorium* sp. and *Monomorium* spp. These two taxa, which are dominant ant taxa in many habitats (Gonalves and Pereira, 2012; Gunawardene et al., 2009; Ślipiński et al., 2012; Stringer et al., 2007), are particularly sensitive to plant diversity and often respond to increasing resource heterogeneity (Stringer et al., 2007). Scherber et al. (2010), in contrast, found that plant diversity decreased ant abundance (supplementary Fig. 1 in Scherber et al. 2010). Yet another study documented a positive correlation between the numbers of ant species and plant diversity in coffee plantations (Perfecto and Snelling, 1995). Our findings are consistent with the latter study in that intercropping with one plant type almost always increased or decreased the abundance of each ant taxon.

The diversification of cropping systems through intercropping often alters arthropod community structure, reduces the numbers of herbivore pests (Baliddawa, 1985), and increases the abundance of generalist predators (Andow, 1991; Song et al., 2010). In our study, however, the intercropping of plantain with two or three other crops failed to consistently increase ant abundance, suggesting that interactions between ant species such as intraguild predation are of primary importance in structuring the ant community. Other studies have shown that intercropping can increase intraguild predation while relative abundance of ant species remain unchanged, (e.g., (Skovgård and Päts, 1996). Ant communities often contain a dominant species that can structure the ant assemblage by interfering with the foraging activity of other species (Savolainen and Vepsäläinen, 1988). Wielgoss et al. (2014) showed that ant species richness and evenness depend on the ecologically dominant species. Thus, the tramp ant, *P. longicornis*, can dramatically reduce ant diversity and abundance where it is invasive (Wetterer et al., 1999). Plant diversity may also change the abundance of dominant species and thereby have a major impact on ant assemblages (Djieto-Lordon and Dejean, 1999). Another alternative hypothesis is that plant diversity may provide favorable habitats for ants and enhance the availability of primary resources and alternative prey for predatory ants. An increase in the availability of alternative prey can change the abundance and the competitive ability of an ant species and thus affect its ability to control pests (Vasconcelos et al., 2008).

4.3. Ant abundance and corm damage by *C. sordidus* larvae

We found that the damage caused by *C. sordidus* larvae to plantain corms was correlated with ant abundance for each of the seven taxa. The correlation was negative for *Axinidris* sp., *Monomorium* spp., *Pheidole* spp., and *Tetramorium* sp., taxa which are mostly omnivorous and predaceous (Hanson and Gauld, 1995), and thus potentially direct predators of *C. sordidus*. The potential of *Pheidole* sp. to control *C. sordidus* was demonstrated in Uganda (Abera-Kalibata et al., 2008), and *Pheidole megacephala* and *Tetramorium guinensee* have been used in the biological control of *C. sordidus* in Cuba (Castineiras and Ponce, 1991; Perfecto and Castineiras, 1998). Single individuals of the invasive ant *Pheidole megacephala* are able to capture a wide range of insects including relatively large prey such as *C. sordidus* (Dejean et al., 2008). For *Camponotus* spp., *Odontomachus mayi*, and *Paratrechina longicornis*, however, ant abundance was positively correlated with corm damage caused by *C. sordidus* larvae. We hypothesize that these species may be involved in intra-guild predation or competition with other predators of *C. sordidus*. Although molecular analysis of gut contents demonstrated that *C. sexguttatus* can consume *C. sordidus* (Mollot et al., 2014), *Camponotus* spp. are considered to be largely scavengers (Hanson and Gauld, 1995), and so we suspect that the trophic link between *C. sexguttatus* and *C. sordidus* may reflect consumption of *C. sordidus* eggs or dead adults. This is consistent with the low detection frequency of *C. sordidus* in guts of this species (Mollot et al., 2014). *P. longicornis* may have only a weak ability to reduce *C. sordidus* numbers because this ant species must recruit multiple workers to capture and transport large prey like *C. sordidus* (Kenne et al., 2005). The positive relationship between *P. longicornis* and *C. sordidus* damage may also reflect the ability of this ant to decrease ant diversity and abundance (Wetterer, 1999). Surprisingly, we found a positive relationship between corm damage and the abundance of the predaceous ant *O. mayi*. In their molecular analysis of gut contents, Mollot et al. (2014) found no trophic link between *O. bauri* and *C. sordidus.* However, we hypothesize that the positive relationship between this species and damage is in part because *C. sordidus* larvae are inaccessible to these large ants. This is consistent with the inferences of Way and Khoo (1992), who concluded that predation on both *C. sordidus* eggs and larvae is required to significantly reduce damage. Abera-Kalibata *et al.* (2008) found that predaceous *Odontomachus troglodytes* can reduce *C. sordidus* numbers below damaging levels, depending on *C. sordidus* population density and life stage distribution. The potential for a given species of ant to control *C. sordidus* may also depend on plantation age, plant diversity, and diversity of other arthropods. Indeed, the epigeal surface structure and plant community may also alter control potential for by affecting ant access to inner parts of the banana corm, and therefore to eggs and larvae of *C. sordidus* (Abera-Kalibata et al., 2008). Because of the relatively long period *C. sordidus* larvae spend in the corm (ca. 2 months),

some of the observed damage might have been caused by larvae hatching from eggs laid before the experiment began or before companion plants were fully established. Thus, our results probably underestimate the regulatory effects of the ant community. Longer-term experiments should be carried out in future, and perhaps on a broader scale to reduce the edge effects.

In summary, intercropping plantain with maize, cocoyam, or gourd did not significantly affect damage to plantain corms by *C. sordidus* larvae but it did increase the numbers of some ant species and decrease the numbers of others. The damage caused by *C. sordidus* larvae was either positively or negatively correlated with the abundance of the seven individual ant taxa. Numbers of *Monomorium* spp., *Tetramorium* spp., *Axinidris* sp., and *Pheidole* spp. were negatively correlated with *C. sordidus* damage and these ants appear to be the best candidates for *C. sordidus* biological control. Finally, crop diversification in the plantain agroecosystem altered the composition of ant communities which, in turn, altered the level of *C. sordidus* damage, but the effect of the individual companion plants on *C. sordidus* abundance remains unclear. Additional, longer-term experiments will be needed to further improve management recommendations.

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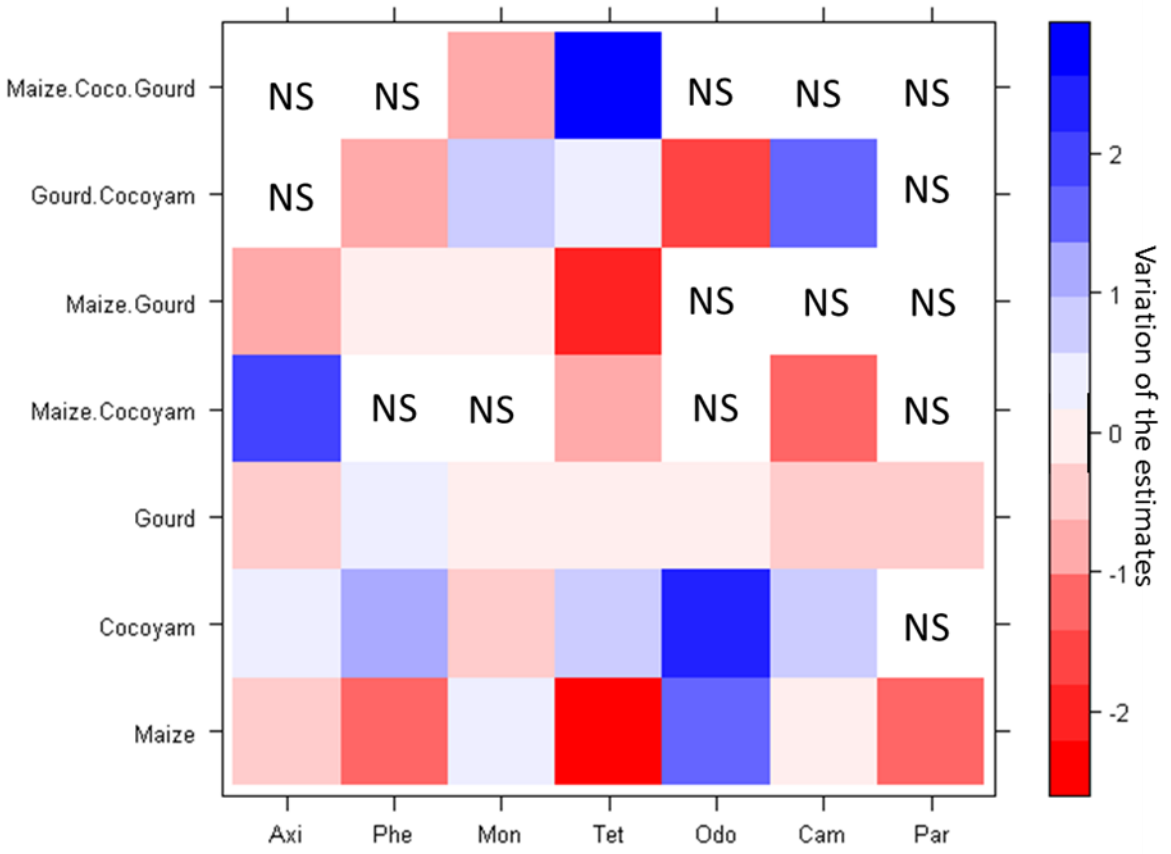

Figure 1. Effects of seven intercropping treatments on ant abundance in a plantain field. Axi: *Axinidris* sp.; Phe: *Pheidole* spp.; Mon: *Monomorium* spp.; Tet: *Tetramorium* sp.; Odo: *Odontomachus mayi*; Cam: *Camponotus* spp.; Par: *Paratrechina longicornis*. The legend on the right presents the variation of the estimates and indicates the direction and strength of the effect of the seven intercropping treatments on ant abundance. Blue indicates positive effects, and red indicates negative effects; the strength of the effect is indicated by color intensity (a darker color indicates a stronger effect) and by the positive and negative values, which indicate the fold-change in ant abundance. NS indicates a non-significant effect of the intercropping on ant abundance. Details regarding the statistical analysis are provided in **Table S1**.

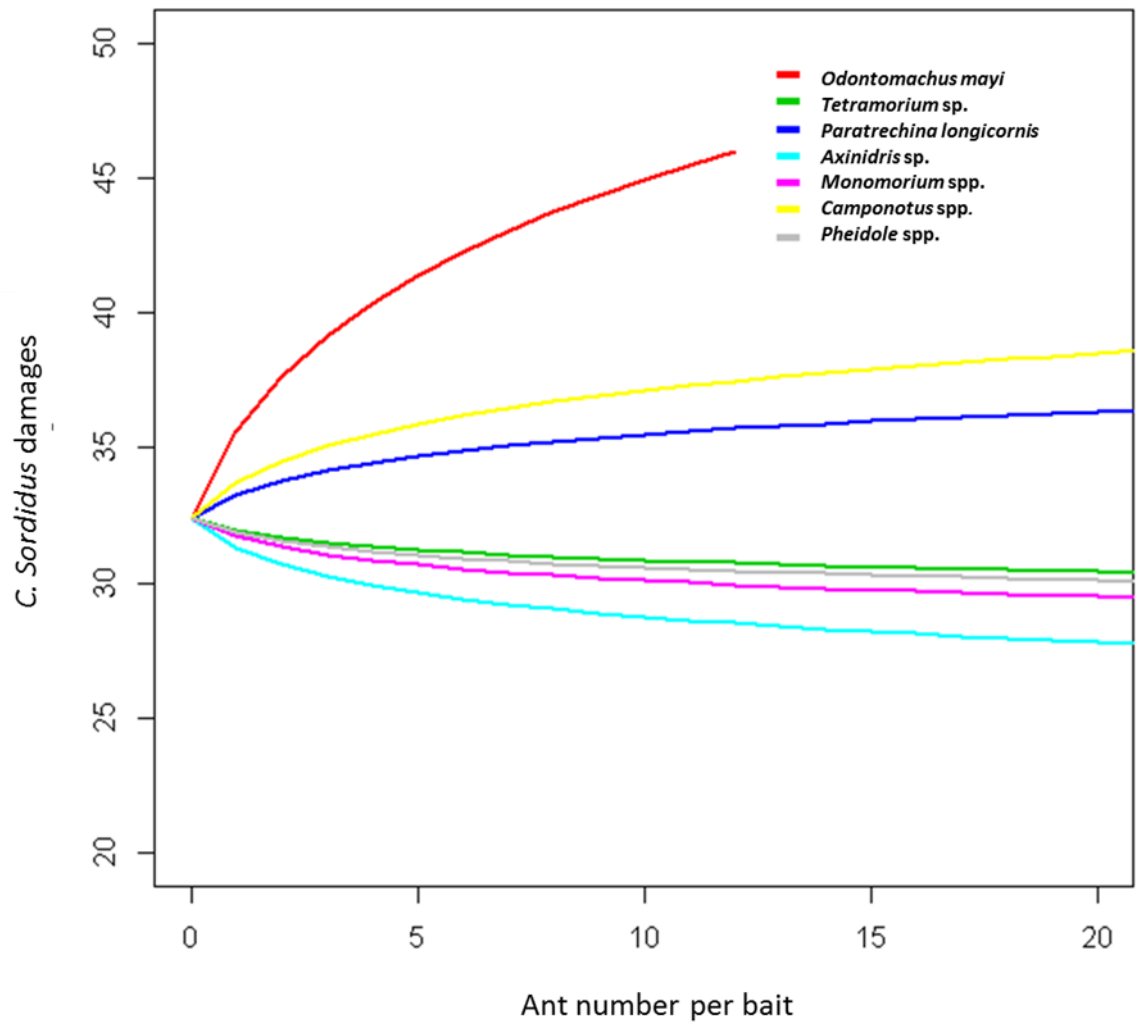

Figure 2. Relationship between damage caused by *C. sordidus* to plantain corms and the abundance of seven ant taxa as predicted by a Poisson GLMM

Table 1. Means and standard errors of ant abundance collected in each treatment

Ant species	Maize	Cocoyam	Gourd	Maize Cocoyam	Maize Gourd	Cocoyam Gourd	Maize Cocoyam Gourd	Control
***Axinidris* sp.**	0.265±0.165	0.75±0.274	0.64±0.236	2.765±0.137	0.265±0.137	0.484±0.229	0.359±0.284	0.5625±0.2615
***Camponotus* spp.**	1.359±0.363	2.25±0.872	0.563±0.243	0.578±0.309	0.969±0.365	3.640±1.515	1.750±0.547	0.6875±0.1780
***Monomorium* spp.**	4.140±1.075	1.530±0.408	2.040±0.434	4.480±1.084	3.010±0.910	3.250±0.968	3.340±0.916	2.4843±0.9085
Odontomachus mayi	0.125±0.085	0.156±0.067	0.015±0.015	0.453±0.212	0.062±0.049	0.030±0.021	0.031±0.021	0.0156±0.0162
Paratrechina longicornis	3.609±0.654	8.609±1.860	6.062±1.043	2.156±0.488	1.984±0.413	7.170±1.330	1.922±0.425	8.7500±1.4524
***Pheidole* spp.**	2.421±0.960	25.180±6.130	12.015±3.340	7.640±2.931	4.156±1.123	10.234±2.254	4.296±0.948	7.1875±2.3397
***Tetramonium* sp.**	0.906±0.350	4.750±2.480	9.734±3.596	0.203±0.132	0.203±0.134	7.437±2.700	0.8437±0.465	10.0156±4.0967

Table 2. Means and standard errors of *C. sordidus* damage index in each treatment, we used the Tukey test to test the statistic differences between the treatments. There are a significant different between the different letters.

Treatments	Mean of damages	Estimate	z-value	Pr(>|z|)
(Intercept)	-	3.383	47.12	< 0.0001 ***
Cocoyam gourd	45.78±5.29a	0.433	10.40	< 0.0001 ***
Maize	42.66±5.40b	0.362	8.58	< 0.0001 ***
Gourd maize	38.28±4.03c	0.254	5.88	< 0.0001 ***
Gourd	34.53±4.17d	0.151	3.42	< 0.0001 ***
Cocoyam	29.06±4.58e	-2.128	-0.46	0.644619
Cocoyam maize	29.69±4.15e	1.588e-07	0.00	0.999997
Gourd maize cocoyam	27.81±4.17e	-0.065	-1.40	0.161974

SUPPLEMENTARY MATERIAL

Table S1. Cumulative abundance, dominance and species richness of ant taxa in plantain plots subjected to seven intercropping treatments.

Ant species	Maize	Cocoyam	Gourd	Maize Cocoyam	Maize Gourd	Cocoyam Gourd	Maize Cocoyam Gourd	Ant dominance (%)
				Rainy season				
***Axinidris* sp.**	0	4	2	3	2	1	2	0.34
***Camponotus* spp.**	2	0	7	5	0	35	1	1.22
***Monomorium* spp.**	73	25	79	32	56	40	79	9.39
O. mayi	3	8	0	29	2	2	4	1.17
P. longicornis	151	172	181	86	60	229	78	23.41
***Pheidole* spp.**	104	1146	412	143	105	376	146	59.50
***Tetramorium* sp.**	46	70	49	3	14	8	12	4.94
Total ant abundance	379	1425	730	301	239	691	322	100
				Dry season				
***Axinidris* sp.**	17	44	39	174	15	30	21	8.08
***Camponotus* spp.**	19	8	1	1	0	0	1	0.71
***Monomorium* spp.**	44	43	39	78	37	36	43	7.60
O. mayi	5	2	1	0	0	0	0	0.19
P. longicornis	80	379	207	52	49	230	63	25.19
***Pheidole* spp.**	41	194	62	313	104	243	154	26.40
***Tetramorium* sp.**	12	234	574	10	1	468	40	31.82
Total ant abundance	218	904	923	628	206	1007	322	100

Table S2. Effects of abundance of each ant species on *C. sordidus* damage to plantain corms.

Ant species	Df	AIC	δAIC	logLik	$\chi 2$	P
***Axinidris* sp.**	8	10717	-9	-5350.7	11.149	0.0008409 ***
***Camponotus* spp**	8	10734	-26	-5359.0	27.674	<0.00001***
***Monomorium* spp**	8	10720	-12	-5352.1	13.948	0.000188 ***
Odontomachus mayi	8	10726	-18	-5354.9	19.424	<0.00001***
Paratrechina longicornis	8	10737	-29	-5360.6	30.833	<0.00001***
***Pheidole* spp**	8	10722	-14	-5353.2	16.064	<0.00001***
***Tetramonium* sp.**	8	10714	-6	-5349.1	7.8382	0.005115 **

AIC: Akaike information criterion, δAIC: variation of AIC, logLik: logarithm of the likelihood.

Table S3. Effect of the seven intercropping treatments on the abundance of seven ant taxa

Treatment	Df	AIC	δAIC	logLik	$\chi 2$	Pr(>Chisq)
			***Axinidris* sp.**			
Null Model	7	1540.2	-367.2	-951.68	381.12	<0.00001***
Maize	4	1648.7	-24.5	-820.35	26.484	<0.00001***
Cocoyam	4	1718.0	-93.8	-855.00	95.778	<0.00001***
Gourd	4	1713.0	-88.8	-852.50	90.789	<0.00001***
Maize + Cocoyam	7	1601.0	-62.7	-793.49	64.681	<0.00001***
Maize + Gourd	7	1540.3	-2	-763.16	4.014	0.04512*
Cocoyam + Gourd	7	1539.9	-1.6	-762.94	3.5704	0.05882
Maize + Gourd + Cocoyam	8	1538.3	1.9	-761.15	0.068	0.7943
			***Camponotus* spp.**			
Null model	7	2856.6	-326.7	-1426.3	340.62	<0.00001***
Maize	4	2705.3	-56.1	-1348.6	58.086	<0.00001***
Cocoyam	4	2773.4	-124.2	-1382.7	126.26	<0.00001***
Gourd	4	2667.1	-17.9	-1329.6	19.94	<0.00001***
Maize + Cocoyam	7	2599.5	-70.1	-1292.7	72.085	<0.00001***
Maize + Gourd	7	2528.0	1.4	-1257.0	0.6308	0.4271
Cocoyam + Gourd	7	2569.7	-40.3	-1277.8	42.305	<0.00001***
Maize + Gourd + Cocoyam	8	2529.4	0.4	-1256.7	1.4423	0.2298
			***Monomorium* spp.**			
Null model	7	4422.5	-64.9	-2209.2	78.836	<0.00001***
Maize	4	4410.8	-11	-2201.4	13.023	0.0003078***
Cocoyam	4	4404.2	-4.4	-2198.1	6.4408	0.01115*
Gourd	4	4405.9	-6.1	-2198.9	8.119	0.00438**
Maize + Cocoyam	7	4371.0	1.9	-2178.5	0.0128	0.9099
Maize + Gourd	7	4398.7	-25.8	-2192.4	27.765	<0.00001***
Cocoyam + Gourd	7	4376.3	-3.4	-2181.2	5.3848	0.02031*
Maize + Gourd + Cocoyam	8	4372.9	-15.3	-2178.5	17.314	<0.00001***
			Odontomachus mayi			
Null model	7	405.18	-40.9	-200.59	54.9	<0.00001***
Maize	4	364.91	-3.01	-178.46	5.0086	0.02522*

Cocoyam	4	374.94	-13.04	-183.47	15.041	0.0001052***
Gourd	4	385.55	-23.65	-188.77	25.645	<0.00001***
Maize + Cocoyam	7	361.36	-1.06	-173.68	1.0638	0.3023
Maize + Gourd	7	360.81	1.49	-173.41	0.5125	0.4741
Cocoyam + Gourd	7	365.3	-0.2	-175.65	5.0029	0.02531*
Maize + Gourd + Cocoyam	8	362.30	1.98	-173.15	0.0165	0.8977
Paratrechina longicornis						
Null model	7	5834.2	-937.6	-2915.1	951.58	<0.00001***
Maize	4	5751.9	-857.6	-2872.0	859.64	<0.00001***
Cocoyam	4	4893.5	0.8	-2442.7	1.1896	0.2754
Gourd	4	4961.6	-67.3	-2476.8	69.27	<0.00001***
Maize + Cocoyam	7	4895.6	-0.5	-2440.8	2.504	0.1136
Maize + Gourd	7	4894.4	0.7	-2440.2	1.3315	0.2485
Cocoyam + Gourd	7	4894.0	1.1	-2440.0	0.9459	0.3308
Maize + Gourd + Cocoyam	8	4895.1	1.5	-2439.5	0.4793	0.4888
***Pheidole* spp.**						
Null model	7	11798.7	-2024.4	-5897.3	2038.4	<0.00001***
Maize	4	11323.4	-1358	-5657.7	1360	<0.00001***
Cocoyam	4	10249.9	-284.5	-5121.0	286.53	<0.00001***
Gourd	4	10023.8	-58.4	-5007.9	60.422	<0.00001***
Maize + Cocoyam	7	9770.7	1.6	-4878.4	0.4429	0.5057
Maize + Gourd	7	9778.8	-6.5	-4882.4	8.5062	0.003539**
Cocoyam + Gourd	7	9958.0	-185.7	-4972.0	187.73	<0.00001***
Maize + Gourd + Cocoyam	8	9772.3	2	-4878.1	0.0102	0.9197
***Tetramorium* sp.**						
Null model	7	7889.8	-2188.7	-3942.9	2202.6	<0.00001***
Maize	4	7861.2	-2057.6	-3926.6	2059.6	<0.00001***
Cocoyam	4	5847.6	-44	-2919.8	45.953	<0.00001***
Gourd	4	5810.0	-6.4	-2901.0	8.379	0.003796**
Maize + Cocoyam	7	5748.4	-7.5	-2867.2	9.4452	0.002117**
Maize + Gourd	7	5753.5	-12.6	-2869.8	14.598	0.0001331***
Cocoyam + Gourd	7	5787.9	-47	-2886.9	48.962	<0.00001***
Maize + Gourd + Cocoyam	8	5740.9	39.8	-2862.5	41.781	<0.00001***

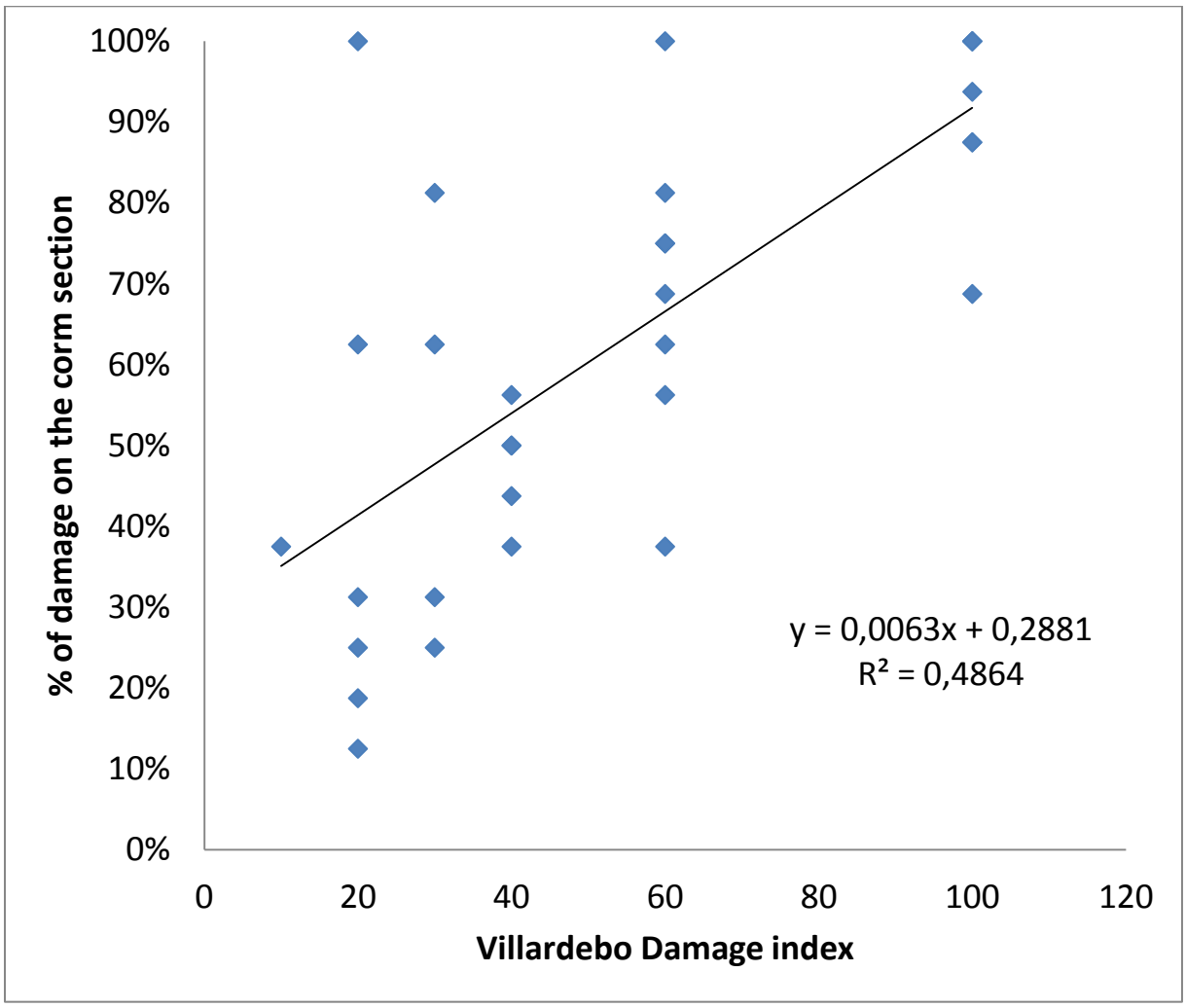

Figure S1. Correlation between the percentage of damage on the corm section and Villardebo damage index. The corm transversal section allowed assessing the damages at surface of the corm. The corm surface was divided in 16 slices and the damaged slices were estimated in percentage. The Villardebo damage index is standard and was used to assess the damages at the periphery of the corms.

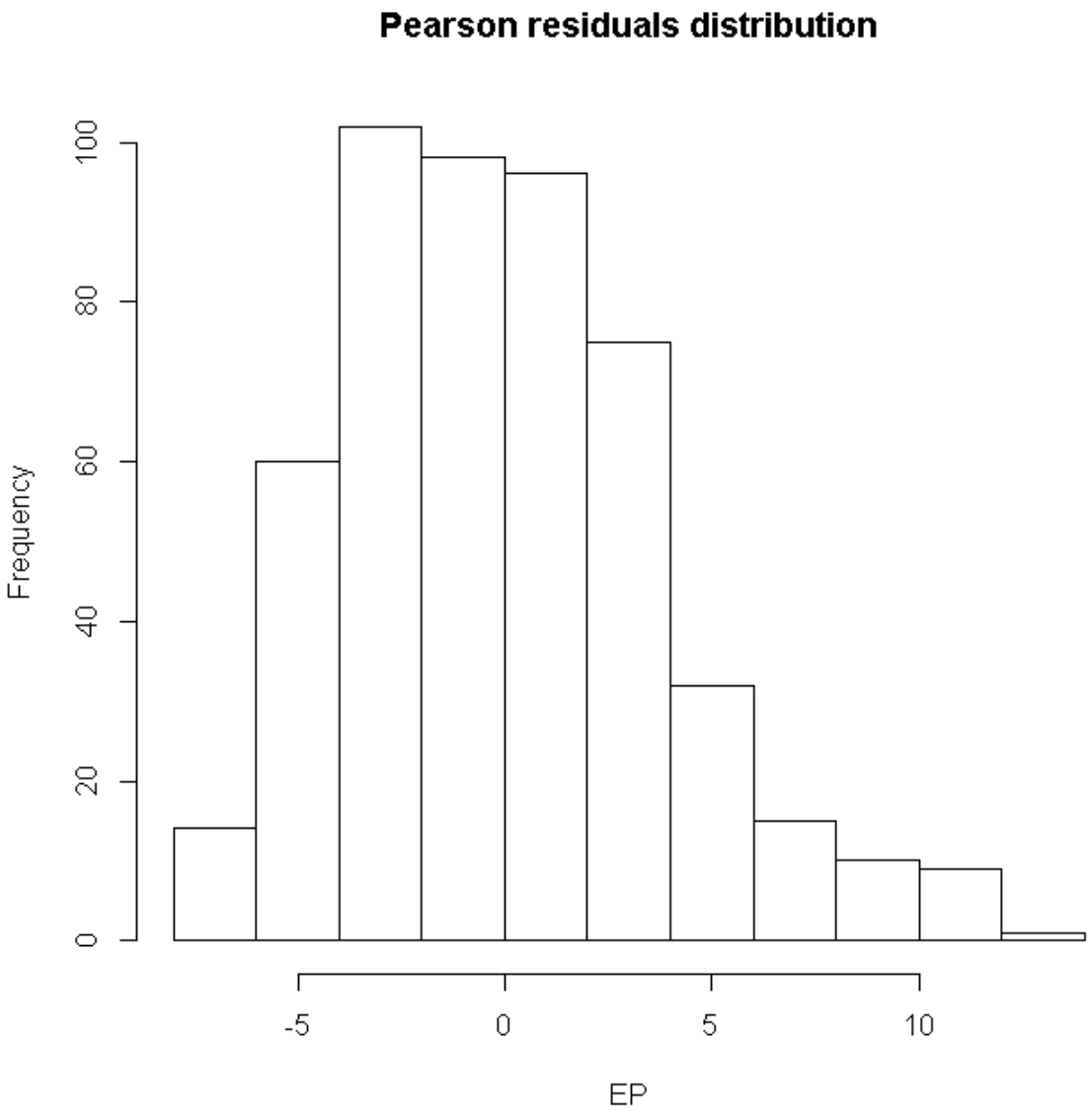

Figure s2: Pearson residuals distribution showing a normal distribution of the model of relationship between *C. sordidus* damages and ant abundance

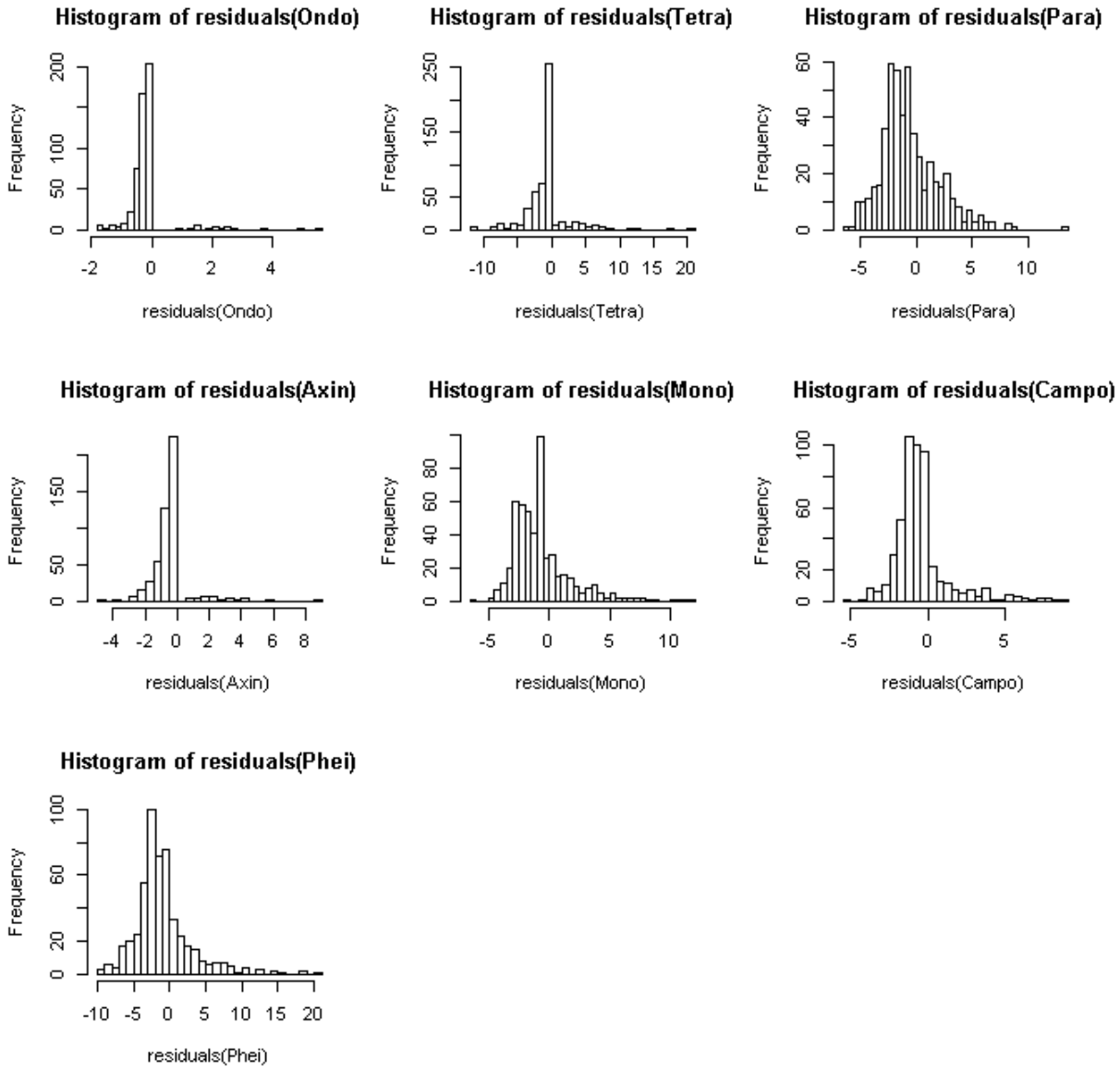

Figure s3. Pearson residuals distribution showing a normal distribution of the model of relationship between the abundance of each ant species and the treatments, Axin: *Axinidris* sp.; Phei: *Pheidole* spp.; Mono: *Monomorium* spp.; Tetra: *Tetramorium* sp.; Ondo: *Odontomachus mayi*; Campo: *Camponotus* spp.; Para: *Paratrechina longicornis*.

Chapitre 4. Discussion générale, conclusion et perspectives

1. Les apports de la thèse

L'objectif général était de comprendre l'effet de la diversité des plantes sur les réseaux trophiques des arthropodes et la régulation des ravageurs par les prédateurs généralistes à l'échelle locale. Premièrement, pour comprendre comment la diversité des plantes modifie la régulation des ravageurs par les prédateurs généralistes à l'échelle locale une méta-analyse a été faite pour expliquer les facteurs liant la diversité des plantes à la régulation des herbivores par les prédateurs généralistes. Deuxièmement, pour comprendre l'effet de la diversité des plantes sur les réseaux trophiques des arthropodes dans les systèmes multi-espèces nous avons caractérisé les communautés des végétaux et des arthropodes. Ensuite en station, dans le but de maximiser la régulation biologique de *C. sordidus* nous avons étudié l'effet de quelques plantes associées au plantain sur les dégâts de *C. sordidus* et les communautés des fourmis.

1.1. Caractériser le réseau trophique

La thèse a permis de décrire le réseau trophique des systèmes de culture à base de plantains aussi bien en termes de composition spécifique que de structure dans les systèmes multi-espèces à base de plantain en milieu paysan. Dans ces systèmes de culture, nous avons caractérisé les communautés des végétaux en identifiant toutes les cultures associées au plantain. Nous avons fait un suivi de la dynamique spatio-temporelle des communautés animales et végétales par des mesures d'abondance en saison sèche et saison des pluies. Dans ces agroécosystèmes, nous avons pris des mesures sur 8325 plantes cultivées (appartenant à 30 espèces). Les parcelles étudiées couvraient une gamme de diversité de cultures (aussi bien en richesse spécifique qu'en diversité fonctionnelle). La caractérisation de la communauté des arthropodes a été réalisée par des mesures d'abondance à l'aide des piégeages réguliers. Pendant les deux saisons, 19.946 fourmis ont été collectées et réparties en 14 taxa de fourmis par le piégeage avec appât. Le second type de piège a capturé 1730 arthropodes comportant 19 taxa d'arthropodes. Globalement, les systèmes multi-espèces à base de plantain semblent comporter un peu plus de taxa d'arthropodes que les systèmes de monoculture avec les mauvaises herbes en Martinique. Tixier et al (2013) ont mentionné 26 taxa d'arthropodes

dans des études réalisées dans les bananeraies de la Martinique, plus de 30 taxa ont été mesurés dans les systèmes plantains étudiés ici. Nos résultats, ne sont cependant pas comparables à des études menés dans des systèmes semi-naturels, par exemple, Haddad et al (2011) ont collecté sur 10 ans 112 238 arthropodes comportant 733 taxa d'arthropodes avec une gamme croissante de diversité de plantes allant jusqu'à 16 espèces de plantes dans des systèmes naturels. La faible diversité d'arthropodes observée dans les systèmes cultivés (même multi-espèces) pourrait être due à la régularité des pratiques agricoles qui perturbent régulièrement la communauté (replantation, sarclage, récolte…). Les pratiques culturales de désherbage semblent particulièrement importantes dans la perturbation des habitats des arthropodes et doit réduire leur diversité.

1.2. Rôle des plantes cultivées sur la structuration du réseau

Globalement, nous avons observé que la diversité des plantes cultivées augmente de l'abondance des prédateurs généralistes et une diminution des herbivores dans les systèmes multi-espèces à base de plantain. Cette relation dépend cependant des groups d'arthropodes considérés. Dans le cas des fourmis nos résultats montrent bien qu'au-delà de la richesse spécifique des plantes cultivées, c'est la diversité fonctionnelle qui semble importante. Ainsi, la structure de la végétation en termes de stratification affecte l'abondance des fourmis. La dominance de quelques taxa de fourmis apparait selon le type de strate des plantes. Nos résultats fournissent les bases qui permettront d'orienter la communauté de fourmis avec la sélection des espèces végétales. Par exemple, pour favoriser les fourmis *Paratrechina longicornis*, *Camponotus* spp., et *Axinidris* sp., qui ont été montré comme des prédateurs potentiels de *C. sordidus*, il semble important de favoriser la strate arborée. Notre étude sur la communauté de fourmis en parcelles paysannes à également permis de mettre en évidence le rôle majeur des interactions interspécifiques pour structurer cette communautés. Des relations d'exclusion et de synergie ont été observées entre plusieurs espèces de fourmis dans les agroéco-systèmes de plantain. Les interactions entre différentes espèces de fourmis montrent l'importance de considérer une approche communauté pour comprendre les mécanismes liant la végétation aux fourmis au lieu de faire des analyses par espèce.

L'expérimentation d'associations d'un nombre réduit de plantes (couramment cultivées au Cameroun) a permis de compléter notre connaissance sur le rôle spécifique de chaque plante associée et de tenter de comprendre la relation entre structure des communautés de fourmis et régulation de *C. sordidus*. Ce dernier point est assez difficile à mettre en évidence dans des parcelles paysannes du fait de l'hétérogénéité des niveaux d'infestation initiaux ; alors que dans notre

expérimentation ce niveau était plus homogène. Dans un système simplifié avec trois cultures associées au plantain, l'effet de chaque plante cultivée et de leurs associations sur l'abondance des fourmis a pu être déterminé. Le maïs a été positivement corrélé à l'abondance des fourmis *Camponotus* spp., *Monomorium* spp., et *Odontomachus mayi*. Nous pouvons supposer que cette relation s'explique par le fait que le maïs peut offrir des habitats et de ressources alimentaires favorables à ces trois taxa. D'autres études on montrés que les ravageurs du maïs constituent des proies pour les fourmis (Perfecto and Sediles, 1992). Il peut également y avoir aussi une interférence entre les fourmis et la présence de certaines espèces de fourmis sur la plante empêche d'autres fourmis d'exercer la prédation sur les ravageurs du maïs (Dejean et al., 2000). Par contre, le maïs a été négativement corrélé avec les taxa de fourmis *Paratrechina longicornis*, *Pheidole* spp., *Tetramorium* sp., et *Axinidris* sp. Cette relation négative pourrait s'expliquer par les pratiques agricoles comme le désherbage manuel (réalisé couramment par les petits agriculteurs dans ces systèmes) qui doit perturber les colonies des fourmis (Folgarait, 1998; Perfecto and Snelling, 1995). Par contre, d'autres espèces de fourmis peuvent ne pas être affectées par les pratiques agricoles si elles s'abritent beaucoup plus sur leurs plantes hôtes.

Notre étude a montré que le macabo était corrélé positivement avec plus de taxa de fourmis que les deux autres plantes associées. Les taxa de fourmis *Axinidris* sp., *Camponotus* spp., *Odontomachus mayi* et *Pheidole* spp., étaient plus abondants dans les parcelles expérimentales où le macabo est cultivé. Le macabo est un tubercule et des études ont montré que les tubercules ont souvent des relations de mutualisme avec les fourmis (Giusto et al., 2001). Le macabo grâce à ses feuilles étalées 'en forme de cœur', abritent plusieurs espèces de fourmis. La face interne des feuilles de macabo constitue aussi un habitat favorable à plusieurs espèces de fourmis lors de conditions défavorables. Dans ce micro-habitat, les fourmis protègent la plante de macabo contre les insectes défoliateurs au niveau des surfaces internes et externes des feuilles de la plante au cours de leur déplacement.

La pistache était seulement corrélée avec *Pheidole* spp. Notre résultat est cohérent avec les études qui montrent que chez les cucurbitacées (dont la pistache fait partie), *Pheidole* sp. est souvent abondant sur les bractées, bractéoles, calices des fleurs des cucurbitacées et les protègent contre les herbivores (Agarwal and Rastogi, 2010). La pistache est une plante herbacée vivace et rampante avec des vrilles spiralées. Elle nécessite moins de pratiques culturales en réduisant les repousses des mauvaises herbes et en favorisant la stabilisation la communauté des arthropodes du sol et de la litière. Cette plante s'étale au sol et crée un microclimat et un micro-habitat qui abrite plusieurs

communautés d'arthropodes dont les fourmis. Ce type d'habitat est favorable aux prédateurs généralistes qui y retrouvent des refuges et proies alternatives.

Notre étude globale du réseau des arthropodes en parcelles paysannes par une approche de simplification en groupes trophiques visait définir des règles générales d'effet de la diversité végétale en limitant les cas particuliers liés à chaque taxa. Nous avons déterminé 5 groupes trophiques d'arthropodes constitués des prédateurs, de deux groupes d'herbivores, du charançon et d'un groupe composé principalement de fourmis. La diversité des plantes favorise le groupe des prédateurs en augmentant leur abondance, la relation semble solide. Elle s'explique probablement par des effets d'habitat et de ressources (plus abondantes et plus variées). Cet effet ressource semble corroborer les résultats obtenus dans des systèmes plus simple, où l'ajout d'une plante de couverture a permis de fournir des proies alternatives aux prédateurs (Mollot et al., 2014; Mollot et al., 2012). L'augmentation de l'abondance des prédateurs dans ces systèmes de culture diversifiés doit logiquement augmenter le contrôle des herbivores. Par contre, le contrôle des ravageurs des cultures ne doit augmenter que si ces derniers sont des proies préférées de ces prédateurs (les herbivores ont une relation de type 'compétition apparente'). L'approche par l'isotope ^{13}C permet en partie d'évaluer la connexion entre les groupes trophiques. En effet, la signature ^{13}C du groupe d'herbivore n°2 (voir le 2ème article de la thèse) suggère que ce groupe pourrait être des proies préférentielles des omnivores (groupes 5) et des prédateurs (groupe 1). A l'opposé, la signature ^{13}C du groupe d'herbivore 4 suggère qu'ils ne doivent pas entrer dans le régime alimentaire des groupes 1 et 5. Le charançon (groupe 3) semble avoir une position intermédiaire. De manière particulièrement intéressante, nous avons observé un effet négatif de la diversité végétale sur le groupe le mieux connecté avec les omnivores/prédateurs, suggérant un contrôle par ces derniers, et à l'opposé un effet positif de la diversité végétale sur le groupe 4 qui est le moins connecté avec les omnivores/prédateurs, suggérant qu'il n'y a pas de contrôle de ces derniers mais sans doute un effet habitat favorable lié à la diversité végétale. Le charançon se positionne encore en situation intermédiaire sans effet significatif de la diversité végétale. Nous pouvons émettre l'hypothèse que l'effet de la diversité végétale sur un groupe trophique donné est le bilan des effets habitat/ressource/top-down et que l'intensité de ces effets dépend notamment de la connexion au sein du réseau. La figure 2 illustre ces différents effets et leur résultante sur chaque groupe trophique.

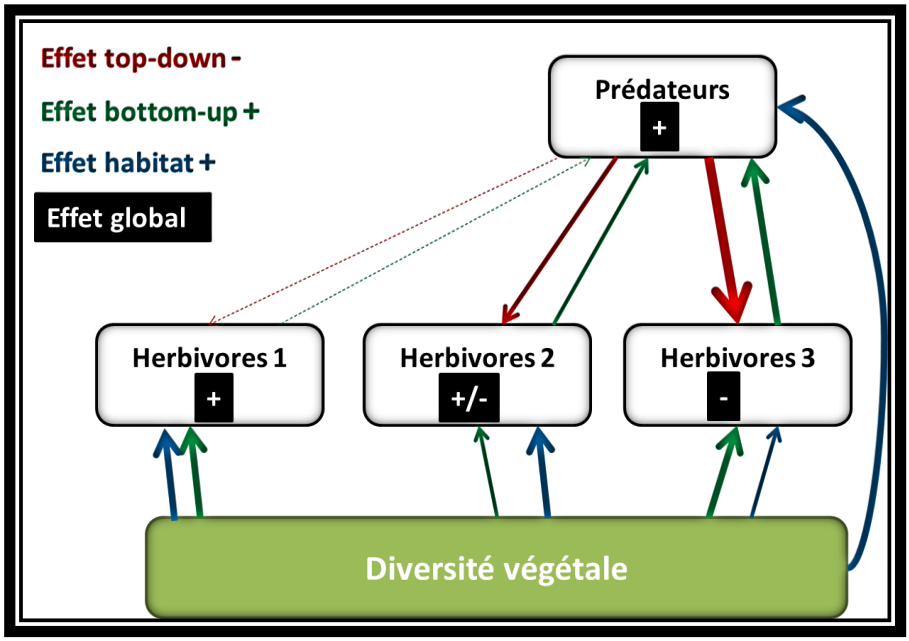

Figure 2 : Schéma synthétique de l'effet de la diversité des plantes sur les différents groupes trophiques couplé à la connectivité du réseau (largeur des flèches)

1.3. Rôle des fourmis dans le contrôle du charançon

Notre étude a montré un effet de la communauté des fourmis sur les dégâts du charançon du bananier. La régulation biologique de *C. sordidus* pourrait être efficace lorsque plusieurs espèces de fourmis exercent la prédation sur le ravageur. Les résultats de cette étude ont confirmé le rôle important des fourmis dans le contrôle de *C. sordidus* dans les bananeraies. Elle a permis d'identifier les taxa de fourmis qui peuvent être associées à la réduction des dégâts des larves de *C. sordidus*. Dans l'agroécosystème de plantain, les taxa de fourmis *Axinidris* sp., *Monomorium* spp., *Pheidole* spp., et *Tetramorium* sp., ont été négativement corrélés avec les dégâts des larves de *C. sordidus*. Ces taxa de fourmis sont des omnivores et ont été reconnus comme de potentiels prédateurs directs de *C. sordidus* (Hanson and Gauld, 1995). Notre étude a montré que les fourmis *Pheidole* spp., ont été les plus abondantes dans les agroécosystèmes de plantain et font partie des espèces qui réduisent les dégâts de *C. sordidus*. Des études d'évaluation expérimentale des impacts de deux espèces de fourmis sur *C. sordidus* en Uganda ont montré le potentiel de contrôle de *C. sordidus* par les fourmis *Pheidole* sp. (Abera-Kalibata et al., 2008). D'autres études précédemment réalisées au Cuba ont montré que *Pheidole megacephalla* et *Tetramorium guinensee* ont été utilisées dans les programmes

de lutte biologique contre *C. sordidus* (Castineiras and Ponce, 1991; Perfecto and Castineiras, 1998). Les mêmes taxa de fourmis suspectés dans notre étude à réguler les populations de *C. sordidus* ont été prouvés être de potentiels prédateurs de ce ravageur. Des analyses moléculaires sur la fourmi *Camponotus sexguttatus* ont montré que cette fourmi consomme *C. sordidus* (Mollot et al., 2014). Les fourmis ont la capacité d'entrer dans le bulbe du bananier par les galeries créées par les larves de *C. sordidus*. Plusieurs études ont montré que les fourmis attaquent et consomment les larves de *C. sordidus* à l'intérieur du bulbe du bananier. L'approche communauté est intéressante pour montrer le rôle des fourmis sur le charançon du bananier. Les différents taxa de fourmis précédemment étudiés dans la régulation biologique du charançon ne sont pas seuls et c'est la communauté dans sa globalité qui participe à la régulation du ravageur. De fortes interactions interspécifiques observées dans la communauté des fourmis dans les agroécosystèmes de plantain enrichissent le potentiel de contrôle de *C. sordidus*. Notre étude a montré que dans les systèmes multi-espèces à base de plantain, plusieurs espèces de fourmis peuvent co-dominer l'agroécosytème. Le comportement de fourragement et de prédation des fourmis est sans doute un élément important dans leur potentiel de contrôle de *C. sordidus*.

2. Retour sur les choix méthodologiques

2.1. Les limites de l'étude des réseaux trophiques par mesures d'abondance et par les isotopes stables

Biais liés au piégeage

Le couplage de piège attractif spécialement développé pour les fourmis avec des pièges d'interception a permis *a priori* d'avoir une bonne représentation de la communauté des arthropodes. Le piège attractif a permis de capturer et d'identifier les arthropodes qui sont associées au charançon du bananier dans les agroécosystèmes de plantain. Le piège avec appât, adapté à la capture des fourmis a permis d'étudier l'abondance et la diversité des fourmis car nombreuses espèces de fourmis sont attirées par des composés protéiques et du miel. Les deux types de pièges utilisés ont aussi des limites. Une des limites des pièges à appât réside dans le fait qu'ils pourraient ne pas attirer toutes les espèces de fourmis de l'agroécosystème. Par exemple, plusieurs espèces de

fourmis arboricoles se retrouvent rarement au sol et ne seront pas attirées par l'appât. Selon l'habitat préférentiel, les fourmis peuvent répondre de manière très différente à la présence de l'appât. Pour des études futures, des pièges à pitfall peuvent être associés aux pièges avec appât afin de maximiser la capture des fourmis. Un autre type de piège peut être aussi placé sur les arbres pour capturer les insectes arboricoles.

Résolution des isotopes stables

Les analyses isotopiques ont permis de faire une simplification en groupes trophiques homogènes des arthropodes. Les analyses isotopiques sont une méthode objective pour constituer les groupes trophiques d'arthropodes. Il est aussi *a priori* possible avec les analyses isotopiques d'identifier les grands types de ressources primaires qui sont à l'origine de la constitution des réseaux trophiques (plante en C3 vs. C4). Dans notre cas, l'isotope ^{13}C permet d'évaluer la connectivité entre groupes trophiques (voir discussion partie 1.2). Les analyses isotopiques ont aussi des limites car elles ne permettent pas de prouver les liens trophiques entre les différents organismes du réseau. Pour des travaux futurs, il pourrait être intéressant d'avoir recours à la biologie moléculaire pour avoir une plus grande résolution dans la description du réseau. Des expérimentations en milieu contrôlé permettraient également d'étudier la régulation du charançon par les prédateurs qui semblent les plus impliqués ; par exemple avec les fourmis *Axinidris* sp., *Monomorium* spp., *Pheidole* spp., et *Tetramorium* sp. Cependant compte tenu de leurs comportements sociaux, la mise en place d'élevage de fourmis n'est pas facile.

2.2. Analyser les communautés

Il existe beaucoup d'études qui recherchent des liens entre quelques espèces mais les approches réseaux/communautés sont assez rares. Ces approches sont importantes car les interactions entre taxa d'arthropodes sont complexes. Par exemple entre fourmis, plusieurs espèces peuvent s'interagir dans l'agroécosystème par une exclusion ou une dominance/codominance de plusieurs espèces de fourmis. L'approche communauté prend en compte les interactions entre les arthropodes alors que considérer seulement une espèce ne permet pas de comprendre comment la régulation peut se mettre en œuvre.

L'analyse de la communauté d'arthropodes, principalement pour les fourmis, s'est fait à l'aide de GLMs. Les GLMs permettent de prendre en compte de manière simultanée les différentes interactions entre taxa et sont particulièrement puissants pour tester des effets entre plusieurs communautés d'organismes. Cependant, il y a des limites à ce genre d'approche car elle devient difficile quand on a beaucoup trop d'espèces. La simplification en groupes fonctionnels semble particulièrement adaptée à l'analyse par GLMs.

3. Perspectives

3.1. Evaluer l'effet de la régulation du charançon à de plus grandes échelles spatiales et temporelles

Les conditions environnementales peuvent influencer les communautés des arthropodes des agroécosystèmes. Les parcelles voisines des champs de culture peuvent modifier l'abondance et la diversité des arthropodes par leur migration d'une parcelle à l'autre. Il semble particulièrement pertinent d'étudier l'effet de l'association des plantes sur la régulation du charançon dans des dispositifs expérimentaux de plus grande taille pour limiter les effets de bordure. La dynamique de la régulation du charançon se met en place sur de longues périodes et il serait donc important de faire des observations rigoureuses pendant plusieurs cycles de culture (3 à 5 ans) afin de déterminer avec précision l'effet de la diversité des cultures sur la régulation du charançon.

3.2. Replacer les interactions au sein de la communauté des arthropodes dans la trajectoire des systèmes de culture plantains

Les cultures associées avec le plantain se font de manière séquentielle selon différentes trajectoires (association avec les cultures annuelles et les cultures pérennes…). Il serait intéressant de mesurer l'importance des régulations dans les différentes phases de ces trajectoires pour évaluer des systèmes de culture plutôt que des associations considérées comme figées.

3.3. Intégrer la dimension de dispersion dans la dynamique des réseaux

La dispersion des arthropodes est logiquement affectée par des patterns spatiaux des plantes présentes dans le système (Pringle et al., 2010). Ces patterns spatiaux sont particulièrement diversifiés dans les systèmes de culture à base de plantains. Une perspective intéressante serait d'intégrer à l'étude de la diversité de plantes sur la structuration de la communauté d'arthropodes à la fois des descripteurs de ces patterns spatiaux et les traits d'histoire de vie des arthropodes (notamment ceux liés à la dispersion). Dans le cas des fourmis, il semblerait particulièrement intéressant d'intégrer dans de futures analyses des informations relatives aux traits liés aux stratégies de fourragement : recrutement de masse, chasse en groupe, solitaire.

3.4. Vers une modélisation de la communauté de plante et d'arthropodes

La modélisation des réseaux trophiques pourrait permettre de porter un regard complémentaire sur la structuration et le fonctionnement des réseaux trophiques des systèmes multi-espèces à base de plantain. Dans ce cas d'étude, elle serait sans doute intéressante pour comprendre la dynamique temporelle des interactions entre les plantes et les communautés des arthropodes. Une piste prometteuse pour modéliser ses systèmes complexes est la simplification en groupes trophiques. Par exemple une approche théorique du mini-réseau présenté dans la figure 2 (dans ce chapitre) pourrait permettre de quantifier l'importance relative des différents effets (habitats/ressource/top-down) sur le fonctionnement de ce réseau et *in fine* sur la régulation des herbivores. Ce type de modèles pourrait simuler, en plus des effets trophiques, des effets non-trophiques (Duffy et al., 2007; Goudard and Loreau, 2008).

4. Conclusion

Ce travail de thèse illustre l'étude de la relation entre diversité biologique, fonctionnement des agroécosystèmes et services écosystémiques. A partir de l'exemple des systèmes multi-espèces à base de plantain, cette étude apporte des éléments concrets sur les mécanismes liant la diversité des plantes cultivées et la structure des réseaux trophiques des arthropodes à l'échelle locale. De façon

générale, cette étude démontre comment les mécanismes de régulation des ravageurs sont influencés par la diversité des plantes et comment la structure et le fonctionnement du réseau trophique des arthropodes peut être liés au service de régulation des ravageurs.

La méta-analyse effectuée au cours de cette thèse a permis de comprendre de façon générale les facteurs qui lient la diversité des plantes à la régulation des ravageurs par les prédateurs généralistes à l'échelle locale. La spécialisation et l'échelle à laquelle la diversité des plantes joue sur les réseaux trophiques des arthropodes sont à prendre en compte pour la gestion des ravageurs dans les agroécosystèmes.

Les expérimentations en milieu paysan ont démontré que les effets de la diversité des plantes sur l'abondance des arthropodes dans les systèmes multi-espèces à base de plantain des milieux tropicaux diffèrent selon les groupes trophiques et l'échelle spatiale. La diversité des plantes augmente l'abondance des prédateurs généralistes et peut diminuer l'abondance des herbivores les mieux connectés avec ces derniers. L'étude à la fois en conditions expérimentales et en parcelles paysannes a permis de mieux comprendre le rôle fonctionnel des plantes associées sur la structuration de la communauté de fourmis. Nos résultats confirment l'importance des fourmis sur la régulation du charançon et de ses dégâts.

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